INTERACTIONS OF RESISTANT CORN CULTIVARS, <u>SPODOPTERA</u> <u>FRUGIPERDA</u> (J.E. SMITH) AND <u>ARCHYTAS</u> <u>MARMORATUS</u> (TOWNSEND)

By

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INTERACTIONS OF RESISTANT CORN CULTIVARS, SPODOPTERA FRUGIPERDA (J.E. SMITH) AND ARCHYTAS MARMORATUS (TOWNSEND)

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Chairperson: Carl S. Barfield
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Measures of consumption, development and fecundity of Spodoptera frugiperda (J.E. Smith) were obtained on diets containing silks of the resistant corn cultivar 'Zapalote Chico'. Field performance of Archytas marmoratus Townsend against S. frugiperda in whorls of Stowell's Evergreen (susceptible corn cultivar) and MpSWCB-4 (resistant corn cultivar) was investigated. Effects of resistant and susceptible corn cultivars on the detoxication enzyme aldrin epoxidase and insecticide susceptibility of S. frugiperda to three classes of insecticides were determined.

Diets containing Z. Chico corn silks inhibited growth of S. frugiperda larvae. Pupal weight and fecundity were reduced as Z. Chico silk content of the diet was increased. There was a significant increase in larval developmental

time from 15 days to 33 days on the control diet and diet containing 20 g of Z. Chico silks, respectively.

Present investigations represent an attempt to study three trophic levels in an agricultural system with a resistant corn cultivar as the producer, S. frugiperda the primary consumer, and A. marmoratus the secondary consumer. Compatibility of a parasitoid as a control method, in combination with resistant varieties, may be erroneously assumed. The host diet may have a potentially deleterious effect on a parasitoid's performance. Performance of A. marmoratus was not affected adversely by S. frugiperda feeding on the resistant corn cultivar. Detoxication enzyme levels increased slightly when larvae were reared on MpSWCB-4, compared to those reared on Stowell's Evergreen. Z. Chico silk diets caused inhibition of the detoxication enzyme. Relative potency of three insecticide classes toward S. frugiperda was pyrethroid > carbamate > organophosphate. S. frugiperda reared on the susceptible cultivar were more susceptible to methomyl and bifenthrin, with LD_{50}'s of 2.39 ug/g larva and 0.45 ug/g larva, respectively, than larvae reared on MpSWCB-4 with LD_{50}'s of 4.19 ug/g larva and 1.29 ug/g larva, respectively. The organophosphate chlorpyrifos was more toxic to larvae reared on MpSWCB-4 than larvae reared on Stowell's Evergreen.

This work is dedicated to my parents Dr. and Mrs. F. Christian Sr., my brothers, Dr. F. Christian Jr. and E. Christian, my nieces and nephews, my husband Henry Meier, my children Fernanda, Jack, Anthea and Rachel.

CHAPTER I

INTRODUCTION

> Pest control is recognized as an integral part of modern agriculture, and necessarily requires the discovery of new information and technology to address evolving pest problems. The fervor for routine applications of pesticides has subsided because of socio-environmental and, recently, economic concerns. These concerns have brought about renewed interest and greater in-depth research on insect resistance in plants and in biological control. While it is generally conceded that these two pest control methods are compatible and among the most important integrated pest management tactics, most of the research in these two fields has been done independently of the other. (Verbatim from the preface, Boethel and Eikenbary 1986)

The above statement holds true for the management of the fall armyworm (FAW), *Spodoptera frugiperda* (J.E. Smith) [Lepidoptera: Noctuidae], on corn, *Zea mays* (L.), in the United States. The more that is understood about the pest regarding its ecology, biology, natural enemies, biochemistry etc., the better the chance of knowing the ramifications of a control method and successfully controlling the pest. The purpose of this project was to investigate some insect-plant interactions among FAW and two resistant cultivars of corn, Zapalote Chico (ZC) and MpSWCB-4. Plant resistance to FAW was reviewed by Wiseman and Davis (1979). Since then, sources of resistance to FAW have

been found in Zapalote Chico and MpSWCB-4 corn. An attempt was made in the present study to evaluate the compatibility of the resistant cultivar MpSWCB-4 and a FAW natural enemy, <u>Archytas</u> <u>marmoratus</u> (Townsend) [Diptera: Tachinidae], in multitactic control of FAW. The effect of FAW feeding on the resistant corn cultivars ZC and MpSWCB-4 and on a detoxification enzyme and subsequent insecticide susceptibility of FAW was studied.

Integrated pest management (IPM) principles serve as guidelines in efforts to manage insect pests (see Barfield and O'Neil 1984; Bottrell 1979).

1. POTENTIALLY HARMFUL SPECIES WILL CONTINUE TO EXIST AT TOLERABLE LEVELS OF ABUNDANCE.

The objective of IPM is to lower pest populations below economically important levels; eradication is not the objective.

2. THE ECOSYSTEM IS THE MANAGEMENT UNIT.

The boundaries of and the couplings among the components of the system must be identified before design and implementation of an IPM program.

3. THE USE OF NATURAL ENEMIES IS MAXIMIZED.

An understanding of how natural enemies work in the system must be acquired so that optimal use can be made of their impact on target pest populations.

4. ANY CONTROL PROCEDURE MAY PRODUCE UNEXPECTED AND UNDESIRABLE CONSEQUENCES.

An ecologically based management strategy is less

likely to result in "negative effects" within the system being managed.

5. AN INTERDISCIPLINARY SYSTEMS APPROACH IS ESSENTIAL.

The assumption is that information collected by various scientists can and will be integrated. (1-5 Verbatim from Barfield and O'Neil 1984, p. 43-45)

The present project was undertaken as an attempt to make a contribution to the management of FAW in corn, one of the world's most widely distributed food plants and the most important crop in the United States.

The Fall Armyworm

The fall armyworm (FAW), *Spodoptera frugiperda* (J.E. Smith), is one of the most important pests of corn in the United States. It is polyphagous, mobile, and annually attacks corn and other crops, especially gramineous species, throughout the southeastern United States. FAW populations can be found during the entire year in south Florida and Texas; this pest migrates from these areas into uninfested regions farther north each spring (Rabb and Kennedy 1979). Luginbill (1928) lists more than 60 host plant species for FAW, but states that the larvae would probably confine their feeding to corn (*Zea mays* L.), sorghum (*Sorghum bicolor* (L.)), and grasses such as Bermudagrass (*Cynodon dactylon* (L.)) if those plants were available. Corn presently is

implicated (Kennedy and Margolies 1985, Wiseman 1985) as the crop that contributes devastating numbers of these migratory moths to infest other major agronomic crops.

Sparks (1979) reviewed the life cycle of FAW. Adult FAW are nocturnal. They move toward host plants suitable for feeding and oviposition at dusk. Eggs are laid in clusters and protected by a dense covering of scales. Masses contain from a few to hundreds of eggs which hatch in 2-4 days at temperatures around 21.1 - 26.7 °C. Larvae consume egg shells as they hatch and feed on host plants until completion of 6 instars. The sixth instar drops to the ground and pupates in the soil at a depth of about 2.54 - 7.62 cm, depending on soil texture, moisture, and temperature. The first 3 instars are small and require less than 2% of the total foliage consumed. The life cycle requires about 30 days at 80 °F (Barfield et al. 1978) (June-August) throughout the southeastern U.S. and around the Gulf Coast states. At colder temperatures, a FAW generation may take 80-90 days.

FAW does not diapause and, therefore, its geographical range in the U.S. in winter is reduced to south Florida and the southern coastal areas of Georgia, Alabama, Mississippi, Louisiana and Texas (Hinds and Dew 1915). In early spring, FAW populations begin to spread northward and westward within the continental U.S. at rates estimated in some years to be about 300 miles per generation. Southerly winds are believed to be an important factor in this annual dispersal.

Single year loss estimates due to FAW in the southeastern U.S. have ranged between $ 30 and 60 million (Sparks 1979).

Pitre (1986) indicates that FAW populations in the southeastern United States are resistant to carbaryl [Sevin®], methyl parathion [Metacide®], trichlorfon [Dylox®], and diazinon [Spectracide®]. Methomyl [Lannate®], seemed to be effective in all areas, but susceptibility in Florida was declining. Tactics such as chemigation (the application of insecticides through irrigation water), as opposed to aerial broadcasting, and the use of synthetic pyrethroids are new methods being adopted to improve the efficiency of chemical control of FAW. As numerous attempts at FAW control fail, a feasible alternative management strategy is sought. Resistant host plants and natural enemies are considered to be premier alternatives to chemical control.

A single tactic (e.g., chemical control) or a combination of tactics (e.g., resistant varieties and natural enemies together) may be adopted in an attempt to manage FAW on corn. Dependence on chemicals alone historically leads to resistance, resurgence and adverse effects on non-target organisms among other problems. Each year in the United States, despite the use of all pesticides and other controls, pests destroy about 37% of all potential crops (Pimental et al. 1978). Sole dependence on chemical control is not a sustainable strategy for pest control.

Resistant varieties and natural enemies, on the other hand, are sustainable strategies that do not pose any of the above-mentioned problems. Understanding the nutritional ecology of the FAW on a host plant, and how this might impinge on natural enemies or affect the efficacy of pesticides, is useful in designing pest control strategies. Tri-trophic interactions occur among corn (the primary producer), FAW (the consumer), and natural enemies at the third trophic level. The role of resistant host plants on FAW feeding, natural enemy attack of FAW, and insecticide susceptibility of FAW will be discussed.

Host Plant Resistance and Natural Enemies

Painter (1951, p.2) defined plant resistance to insects as ". . . the relative amount of heritable qualities possessed by the plant which influence the ultimate degree of damage done by the insect". He also points out that in order to be a useful character, resistance must be inherited. Resistance is relative, and various degrees of resistance can be recognized (e.g., immunity, high resistance, low resistance). The mechanisms generally accepted and used frequently by entomologists studying plant resistance to insects are those proposed by Painter (1951): non-preference, antibiosis and tolerance. These three mechanisms may be of a physical or chemical nature, and there are many factors that 'condition' all of the mechanisms: (1) how the insect utilizes the plant or plant

parts for food, shelter or oviposition; (2) whether adults and larvae use the same plant for food; (3) features of the environment such as temperature; and many others. A review of the state-of-the-art of plant resistance to FAW was presented by Wiseman and Davis (1979).

The mechanisms of resistance can have a direct effect on the feeding behavior of an insect pest. Antibiosis includes those adverse effects on the insect's life history which result when a resistant variety is used for food (Painter, 1951). Measured effects of resistance may be in the form of death in the early instars, small size or low weight, abnormal longevity, low food reserves, reduced fecundity, death in the prepupal stage, and abnormal behavior (Owens, 1975). A resistant variety may possess adequate food supply and provide all necessary nutrients, while a susceptible variety may be lacking in a necessary diet substance. An insect may therefore gorge itself, destroying or consuming the susceptible host plant, to meet its dietary needs. This statement is somewhat counter-intuitive, but explains to an extent differences in consumption rates for insects feeding on resistant, versus susceptible, varieties of plants. Furthermore, a resistant variety may lack some qualities which provide the attractive stimulus in susceptible varieties, and resistant varieties may possess repellant qualities which can compete with or mask an attractant (Wiseman et al. 1983). Wiseman et al. (1983) state that these characteristics make plant

resistance to insects the most useful of all integrated controls. Wiseman (1985) reviews the mechanisms and types of plant resistance. Several corn genotypes have been identified as having resistance to the FAW (Wiseman et al. 1981, Williams et al. 1983). 'Zapalote Chico' 2451 # (PC3) is a dent corn resistant to silk and ear feeding in the field. A dent corn is the commercial classification of corn characterized by a depression in the crown of the kernel caused by unequal drying of the hard and soft starch making up the kernel. Some of the highest levels of resistance known in corn have been found in the silks of 'Zapalote Chico' (ZC) corn (Straub and Fairchild 1970; Wiseman et al. 1976,1977, 1978). Investigation into the feeding and developmental responses, which will define the phytochemical nature of the resistance, has been attempted. Wiseman et al. (1984) developed and used a laboratory bioassay to evaluate feeding responses of FAW to ZC. Wiseman and Widstrom (1986) reported the mechanisms of resistance of ZC corn silks to FAW larvae, indicating that antibiotic factors present in the silks result in the production of small larvae, small pupae and longer life cycle compared with those fed silks of the susceptible sweet corn 'Stowell's Evergreen'. An attempt was made to investigate the effect of the resistant cultivar 'Zapalote Chico' on FAW feeding, growth, development and fecundity.

Biological control, abbreviated "biocontrol" involves importation, conservation, and/or encouragement of

parasites, parasitoids and predators to reduce pest densities to a level below the economic injury level, and (ideally) maintain them there. Applied biocontrol implies active intervention with biotic components of agroecosystems (Horn 1988). Successful biocontrol is relatively safe, permanent and economical after the initial investment.

The concurrent use of plant resistance and biological control is compatible in principle since both aim at suppression of the insect pest population. However such plant-pest-natural enemy interactions are rarely investigated. In the present study a second resistant cultivar, also thought to be resistant via antibiosis, MpSWCB-4, was used to study the effect of a resistant cultivar on a natural enemy of FAW, *Archytas marmoratus* (Townsend) (Diptera: Tachinidae), in the field. *Archytas marmoratus* (AM) is a primary larviporous, larval-pupal parasitoid of FAW and other noctuids in North and South America and in the West Indies (Sabrosky 1978, Ashley 1979). Findings by Gross et al. (1976) and Pair et al. (1986a), from collections of 5th and 6th instars of the corn earworm, *Helicoverpa zea* (Boddie), and FAW larvae on corn, revealed that AM is a major parasitoid of these species, especially in south Georgia and north Florida. It has since been reared successfully on a large scale using maggots extracted mechanically from fecund females (Gross and Johnson, 1985). Some research has been done on possible detrimental effects of plant antibiosis on biological control agents of various

insect pests including the FAW. *Helicoverpa zea* has an ichneumonid parasite, *Hyposoter exiguae* (Viereck). Campbell and Duffy (1979) found this parasite could be poisoned by an antibiotic (α-tomatine) from resistant tomato plants. Even though α-tomatine is useful in controlling tomato pests, it has an adverse effect on the natural enemy, *H. exiguae,* preventing the parasitoid from exerting an additional pest population regulation effect. This is an example of potential incompatibility of a resistant variety and biological control. The antibiotic in the resistant plant protects the insect from its natural enemy by serving as a prophalactic against the parasitoid. Yanes and Boethel (1983) found that the introduced parasitoid, *Microplitis demolitor* Wilkinson, in the soybean looper, *Pseudoplusia includens*, greatly reduced larval weight and leaf consumption for loopers reared on soybean resistant variety PI 227687. Here, the resistant host plant synergizes the effect of the natural enemy and proves to be compatible with the biological control agent. Isenhour and Wiseman (1989) studied parasitism of FAW by *Campoletis sonorensis*, affected by host feeding on silks of ZC. Wiseman et al. (1983) looked at the influence of resistant and susceptible corn silks on selected developmental parameters of the corn earworm. Isenhour et al (1989) reported enhanced predation by *Orius insidiosus* (Say) on larvae of FAW and corn earworm caused by prey feeding on the resistant corn genotypes MpSWCB-4 and ZC. The influence of resistant plants on

interactions between insect herbivores and natural enemies must be studied to determine compatibility.

Chemical Control

Most insecticides exert a density-independent effect on insect populations. Application of a chemical control usually results in populations below an economic injury level (EIL), the lowest pest population density which will cause economic damage; however, population density is not regulated about a mean, as is (ideally) the case with biological control. If the population is not reduced sufficiently, re-application of insecticides becomes necessary to achieve low densities of pests.

Insecticides presently are the chief weapon against insect pests. Chemical control is the most widely used single technique to reduce densities of insect pests. An advantage of using insecticides is that the proper insecticide, properly applied at the right time, nearly always causes swift death to insects in the treated area. They are useful in emergencies, when a rapid reduction in insect population density is necessary to prevent serious economic loss.

There is an ongoing search for alternative methods of pest control in corn and other crops, but predictably, insecticides will be used on a large scale, world wide, for some time to come (Kumar, 1984). It is therefore necessary

to understand interactions of pesticides with other pest management tactics.

Mixed function oxidases (MFO), located in the endoplasmic reticulum of cells, play an important role in the metabolism of xenobiotics such as insecticides. A detailed review of the functional role of MFO in insects has been published by Hodgson (1983a). This system is thought to be partially responsible for the selective toxicity of insecticides, the development of resistance and the degree of herbivore polyphagy. The effects of host plants on the MFO has been researched by Yu (1982a). Host plants have been reported to affect both the insect's detoxification system and its susceptibility to pesticides. Yu (1982a) found corn-fed FAW to be more tolerant of certain pesticides than soybean-fed FAW. The present study investigates the effect of two resistant corn cultivars on the MFO of FAW and on susceptibility of FAW to three groups of insecticides - a carbamate, an organophosphate and a synthetic pyrethroid. Pesticides frequently are components of pest management programs in corn, so knowing the factors that influence efficacy, which can vary as a function of host plant and nutritional status (Kea et al. 1978, Berry et al. 1980, Yu 1982a) is useful.

Interactions Among Three Trophic Levels

Price et al. (1980) described the influence of plants on interactions between insect herbivores and natural enemies. Terrestrial communities are composed of at least three interacting trophic levels: plants, herbivores, and natural enemies of herbivores. Price et al. (1980) argue that theory on insect-plant interactions cannot progress realistically without consideration of the third trophic level. Plants have many effects, direct and indirect, positive and negative, not only on herbivores but also on the enemies of herbivores. The third trophic level must be considered as part of a plant's battery of defenses against herbivores.

There are several theories on interactions among plants, herbivores and natural enemies of herbivores; however these theories are rarely viewed in the same context or even in the context of how they apply in agroecosystems. The theory of plant chemical defense, as developed by Feeny (1975, 1976), permits some predictions about the efficacy of the herbivores' enemies as influenced by the life history of the plant. Feeny (1976) points out that any plant condition that lowers the growth rate of an insect herbivore makes it available to natural enemies for a longer period and raises the probability of mortality. For example, where insects fed on plants containing tannins and other digestibility reducers; lowered digestibility of food was compensated partially by prolonged feeding. He argues that plants with

digestibility reducers, should support herbivores that are more heavily attacked by enemies, than herbivores on plants without digestibility reducers. Agroecosystems have made previously non-apparent plants more apparent to insects and have provided habitats with high resource availability. Increased herbivory has been the predictable result.

Aspects of interaction between plant genotypes and biological control were discussed by Bergman and Tingey (1979). They emphasize that, as resistant cultivars become more widely used in pest management, their compatibility with biological control agents must be given serious consideration. The concurrent use of resistant cultivars and natural enemies can provide density-independent mortality in times of low pest density and dynamic density-dependent mortality in times of pest increase (resistant cultivars can exert density-independent mortality on the pest while natural enemies exert dynamic density-dependent mortality). Numerous studies indicate that predator and parasite performance may be altered by the host plant of the prey (e.g., Flanders 1942, Smith 1957). Painter (1951) discussed 2 ways in which plant resistance can influence natural enemies. A reduction in prey population may affect the success of some predators and parasites if prey density falls below the optimum searching capacity of the natural enemy. Secondly, host plant-induced changes in prey physiology and behavior may modify the success of natural enemies. The purpose of this study was to investigate

specifically, relationships among FAW, resistant cultivars of corn and a natural enemy of FAW, in the context of pest management.

CHAPTER II

CONSUMPTION, DEVELOPMENT AND FECUNDITY OF FAW ON DIETS CONTAINING SILKS OF THE RESISTANT CORN CULTIVAR 'ZAPALOTE CHICO'

Introduction

The mechanisms of plant resistance generally accepted and used by entomologists in insect plant resistance studies are those proposed by Painter (1951): preference/ nonpreference, antibiosis and tolerance. Antibiosis effects may take the form of death in the early instars, small size or reduced weight, abnormal longevity, low food reserves, less fecundity, death in the prepupal stage, and abnormal behavior (Owens, 1975). Antixenosis is a term used for nonpreference, by which feeding or oviposition may be delayed or prevented (Wiseman, 1985) by either absence of a stimulant or the presence of a deterrent.

A review of the history and the state-of-the-art of plant resistance to FAW was presented by Wiseman and Davis (1979). Wiseman and Widstrom (1986) reported that both nonpreference and antibiosis resistance to feeding are manifested in the silks of Zapalote Chico (ZC) corn to *Helicoverpa zea* (Boddie). Silks of ZC 2451 have been demonstrated to cause high mortality of FAW by the 10th day

of larval feeding. Wiseman and Widstrom (1986) reported that antibiotic factors in the silks result in production of small larvae, small pupae, and longer life cycle compared with those fed silks of Stowell's Evergreen (SEG) sweet corn. They found that larvae fed a diet of 80 g (fresh weight) susceptible silks weighed 246 mg compared with only 4 mg for those fed ZC silks. A high degree of nonpreference also was indicated. Waiss et al. (1979) found high levels of a flavone glycoside, maysin, in ZC.

Slansky (1982) describes the paradigm where insects may alter performance to reach maximum possible fitness. Alterations in performance may involve compensatory responses; for example, altering consumption rate and/or food utilization to obtain sufficient nutrients to reach some minimum weight required to stimulate ecdysis (Slansky and Scriber 1985). Antibiosis, as caused by feeding on ZC, may stimulate some compensatory response in FAW.

Reported here are experiments to determine the effects of silks of the resistant corn cultivar ZC on fall armyworm larval growth, development and fecundity. The method of Blau et al. (1978) was used to separate the effects of feeding inhibition and toxicity leading to antibiosis, the suspected mechanism of resistance.

Materials and Methods

Insects

FAW eggs were obtained from a colony maintained on a pinto bean meridic diet (Perkins, 1979) at the Insect Biology and Population Management Research Laboratory, Tifton, Georgia. Neonate larvae were reared on experimental diets. One neonate larva was placed in each cup, and the cup was sealed with a paper lid. Thirty cups of each diet were set up. The cups were maintained at 26.7 ± 2 °C, at least 75% RH and 14L:10D. Daily observation allowed records to be kept of the duration of each instar and of any mortality. Fresh weights of newly molted fifth instars were taken, and fresh food fed to them was weighed to allow measurement of food consumption. Percent dry weight of the initial diet fed was determined by noting the fresh weight of 5 samples of each of the five diets, drying for 48 hours in the oven at 60 ± 1 °C and re-weighing. Pupae were removed within 8 hours of pupation, dried and weighed. Feces and uneaten diet were collected, dried and weighed to obtain their respective dry weights. A Mettler H35AR balance, accurate to 0.1 mg was used for all weights. All material was dried at 60 ± 1 °C for at least 48 hours.

Experimental Diet

Two corn genotypes were selected: cv. Stowell's Evergreen, a sweet corn susceptible to silk and ear feeding in the field by *Helicoverpa zea* (Boddie) larvae, and cv.

Zapalote Chico 2451# (PC3), a dent corn resistant to silk and ear feeding in the field. The corn used in this experiment was grown in, single-row-plot plantings, 6.1 m long and 0.76 m apart, at Tifton in 1987 according to agronomic practices common to the area.

Diet prepared as follows was provided by Dr. B. Wiseman of the USDA laboratory in Tifton Georgia: Silks of each genotype were harvested 2 days after emergence from the husk leaves. They were excised at the tip of the ear, bulked, and oven dried at 41 $\pm 3°$ C for about 10 days, then ground to a fine powder (1.0 mm screen) using a Cyclotec TC1093 (Fisher Scientific, Atlanta) sample mill. Dry silks were stored in a freezer at -10 $\pm$ 0° C until prepared for use. One concentration of the SEG silk diet was prepared to serve as a susceptible diet check. This contained 5 g of SEG silks in diluted pinto bean diet (300 ml diet : 100 ml distilled water) (Burton 1967). The control diet contained no silk. Three concentrations of ZC silk diet were prepared: 5 g, 10 g, and 20 g. The silk-pinto bean diets were dispensed into 30 ml plastic diet cups, 10 ml per cup, and allowed to solidify for about 2 hours.

Quantitative Performance Studies

Larval food consumption, growth and food utilization indices were calculated, using gravimetric techniques based on dry weights (Slansky and Scriber 1985) in 1988. Performance indices included: larval period (days), day 1

pupal dry weight, dry weight gained during the last instar, food utilization efficiencies (AD = Approximate digestibility, ECD = Efficiency of conversion of digested food, and ECI = Efficiency of conversion of ingested food), relative growth rate (RGR) and relative consumption rate (RCR). These parameters and their interrelationships are defined in the appendix (after Finke 1977). Experimental results were analyzed using the GLM procedure and Tukey's studentized range test ($p=0.05$) to separate means (SAS Institute Inc. 1989).

Toxicity/Feeding Inhibition Test

Unequivocal demonstration of toxicity is often hampered by the behavioral responses of experimental insects, and slow growth does not necessarily indicate adverse effects on metabolism, but possibly a result of behavioral inhibition of feeding (Waldbauer 1962). Blau et al. (1978) describe a technique that permits clearer distinction between feeding inhibition and toxicity. This method was used to separate the effects of feeding inhibition and toxicity leading to antibiosis, the suspected mechanism of resistance for ZC silks.

Twelve newly molted 6th instar FAW larvae reared from eggs were weighed individually, placed in individual petri dishes and fed a quantity of pinto bean check diet to determine an approximate fresh weight consumed in 24 hrs. A calibration curve for final instar larvae reared from eggs

on the check pinto bean meridic diet was obtained by offering groups of 6 newly molted 6th instar larvae different amounts of diet, ranging from none at all, approximately 25%, 50%, 75%, and more than the amount previously determined to be consumed within 24 hours. All of the larvae were set up individually in petri dishes. (Percentage fresh weight of both diet and larvae were determined by obtaining fresh weights of 5 samples of diet and 10 individual larvae and oven drying these as previously described). Larvae were left to feed and then both they and any remaining diet weighed after 24 hrs. Resultant data were used to determine the regression slope of growth rate on consumption rate for the check diet.

Groups of 12 newly molted 6th instar larvae, reared from eggs on the check diet, were then individually weighed and fed the check diets and test diets containing SEG and ZC silks for 24 hrs., in individual petri dishes (1 group per diet). Relative growth and relative consumption rates were calculated and plotted relative to the calibration curve for the check diet.

Fecundity Studies

Thirty FAW larvae were reared individually, in 30 ml plastic diet cups until pupation on a pinto bean diet and on SEG and ZC silk diets as previously described. Pupae were removed and sexed. Separate sexes were placed in Plexiglass™ cages (45x40x40 cm). Upon emergence, males and

females were paired, (10 pairs were set up per diet) and placed in oviposition cages (screen cylinders 20 cm x 9 cm) and supplied 'Bounty™' hand towel paper as an oviposition substrate. The paper towel was secured by a rubber band over the top of the cage. Moths were provided a 10% sucrose solution. All oviposition cages were held in a rearing chamber (Percival™ incubator model I-35LLs) at 26.0 ± 1° C and 90% RH. Oviposition substrates were removed every second day, and replaced. All surfaces, the oviposition substrate, and the sides of the cage were checked for eggs and all eggs counted under the microscope.

Eggs were counted under the microscope with the aid of a fine forceps and a hand held dissecting pin to separate eggs within a mass. Experimental results were analyzed using the GLM procedure of SAS (SAS Institute Inc. 1989).

Pupal Weight Study

FAW larvae were reared on the five diets as described, individually, until pupation. Thirty-six pupae were removed from cups within 24 hours of pupation, sexed and weighed. Percent dry weight of pupae was determined by obtaining fresh weights and oven drying a sample of 10 pupae of each sex from each diet for 48 hrs at 60° C. Experimental results were analyzed using the GLM procedure and Tukey's studentized range test to separate means, since this test is moderately conservative (SAS Institute Inc. 1989).

Results and Discussion

Tables 1 and 2 summarize the developmental parameters for FAW reared on the pinto bean check (CK) diet, the SEG silk and the ZC silk diets. By incorporating three different quantities of ZC silks into the diet, a gradient of resistance was created, to facilitate the observation of the effects on larval mortality and developmental time. Effects of a "low dose" or "high dose" of any allelochemical or antibiotic factor should have been observed at the two extremes, ZC-5 g and ZC-20 g.

Larval Mortality and Developmental Time

Developmental time for FAW larvae (1st instar to pupation) varied on the diets containing silks of SEG and ZC. Larvae reared on the pinto bean check diet (which did not contain any silks) had the shortest developmental time of about 15 days (Figure 1). Larval duration was about 17, 21, 23, and 33 days on the SEG, ZC-5, ZC-10, and the ZC-20 diets respectively. Larvae fed the SEG and the ZC-5 g silk diets had progressively longer developmental times; the differences were statistically significant. There was a significant increase in developmental time to about 23 days and 33 days when larvae fed on ZC-10 g and ZC-20 g silk diets, respectively. There was no significant increase in larval duration for larvae fed ZC-5 and the ZC-10 diet. The ZC-20 g diet caused a twofold increase in developmental time when compared to the check diet.

TABLE 1. Developmental parameters of FAW 5th and 6th larval instars feeding on diets containing silks of a resistant corn cultivar Zapalote Chico and a susceptible cultivar Stowell's Evergreen.

Diet	Developmental Parameters[a]					
	Bi	Bf	B	MB	I	F	T
Pinto bean (check)	5.94 a (0.22)	76.26 a (1.70)	70.32 a (1.67)	27.47 a (0.59)	517.41 a (16.73)	278.53 a (8.10)	6.04 d (0.07)
Stowell's Evergreen	4.66 b (0.21)	65.41 b (2.33)	60.75 b (2.26)	22.91 b (0.75)	377.61 b (15.13)	260.24 a (12.10)	7.08 c (0.06)
Zapalote Chico-5 g	5.56 ab (0.33)	65.56 b (2.23)	60.00 b (2.30)	24.09 b (0.12)	545.99 a (39.73)	243.04 a (13.17)	8.91 b (0.21)
Zapalote Chico-10 g	5.97 a (0.29)	60.48 b (2.65)	54.51 b (2.71)	23.39 b (0.12)	394.08 b (39.73)	263.15 a (13.17)	9.18 b (0.27)
Zapalote Chico-20 g	5.42 ab (0.29)	43.97 c (2.40)	38.55 c (2.35)	18.30 c (0.80)	495.24 ab (67.33)	265.14 a (17.79)	16.21 a (0.57)

[a] Parameters defined in Table A-1. Values expressed as mean (+/- std. error); in columns, values not followed by the same letter are significantly different ($p < 0.05$; Tukey's studentized range test). All weights in mg. Sample sizes were 24 (check), 24 (SEG), 23 (ZC 5 g), 17 (ZC 10 g), 19 (ZC 20 g).

TABLE 2. Fifth instar to pupation feeding efficiencies, consumption and growths for fall armyworm larvae reared on diets containing silks of a resistant corn cultivar Zapalote Chico and a susceptible corn cultivar Stowell's Evergreen.

	Developmental Parameters[a]				
Diet	RGR	RCR	AD	ECD	ECI
Pinto bean (check)	0.43 a (0.01)	3.15 a (0.12)	0.45 b (0.02)	0.32 b (0.02)	0.14 a (0.00)
Stowell's Evergreen	0.37 b (0.01)	2.36 b (0.09)	0.31 c (0.02)	0.60 a (0.06)	0.16 a (0.01)
Zapalote Chico - 5 g	0.28 c (0.01)	2.60 b (0.13)	0.55 a (0.02)	0.21 c (0.01)	0.11 b (0.00)
Zapalote Chico - 10 g	0.26 c (0.01)	1.84 c (0.17)	0.28 c (0.04)	0.53 a (0.07)	0.15 a (0.01)
Zapalote Chico - 20 g	0.13 d (0.01)	1.65 c (0.16)	0.41 b (0.03)	0.24 bc (0.02)	0.09 c (0.01)

[a] Parameters defined in Table A-1. Values expressed as mean (+/- std error); in columns, values not followed by the same letter are significantly different ($p < 0.05$; Tukeys studentized range test). All weights in mg. Sample sizes were 24 (check), 24 (SEG), 23 (ZC-5 g), 17 (ZC-10 g), 19 (ZC-20 g).

Comparing the time to develop from the 5th instar to pupation on the silk and CK diets, larvae fed on the ZC-20 g silk diet took 16 days to pupate compared with 6, 7, or 8 and 9 days respectively on the CK, SEG and ZC-5 and ZC-10 diets, respectively (Figure 2). This was consistent with the pattern observed for overall developmental time for the different diets. There was a significant difference in time to develop from 5th instar to pupation for larvae fed the CK and the SEG diet. Development time from 5th to pupation for larvae fed ZC-5 and ZC-10 diets were not significantly different using Tukey's studentized range test to separate means. Table 1 summarizes the data for the developmental parameters of fall armyworm larval instars feeding on diets containing silks of Zapalote Chico and Stowell's Evergreen. Sample sizes and results of Tukey's studentized range test are indicated on all tables.

Mortality was not significantly different for the different diets. Percent mortality was 3%, 6%, 3%, 6% and 6% for larvae fed the CK, SEG, ZC-5, ZC-10, and ZC-20 silk diets respectively. Some of the larvae died from drowning in water that had condensed in the growth chamber as a result of using a humidifier within the chamber. Percent mortality on the different diets is presented in Table A-2. Differences in sample sizes in the materials and methods and sample sizes used in statistical analyses were due to deaths from drowning, and larvae sacrificed by being weighed and dried to obtain dry weight percentages.

Larval Weights

Figure 3 indicates that there was a progressive decrease in fresh weight of 5th instar FAW larvae reared on the various ZC silk diets; however, these were not significantly different.

Percentage dry weights for 5th instar larvae reared on the different diets are presented in Figure 4. There was no indication of a significant difference in larval percent dryweight between the CK and the various ZC silk diets. Fifth instar larvae fed the SEG silk diet had a significantly higher percent dry weight than larvae reared on all the other diets.

Pupal Weights

Figure 5 shows the mean pupal fresh weights of FAW reared on diets containing Zapalote Chico silks. Pupal fresh weight decreased significantly as the quantity of ZC silk increased in the diet (Tukey's studentized range test). There were significant differences found in pupal dry weights for the different diets (Figure 6). Pupae from the CK diet had the highest dry weight. Dry weight of the CK, SEG and ZC-5 g pupae were similar (no significant differences). Dry weight of pupae from the ZC-10 g diet was significantly lower than the dry weights of pupae from the CK, SEG and the ZC-5 g diets, and significantly higher than dry weight of pupae from the ZC-20 g diet. As ZC silk concentration in the diet increased to 20 g, pupal dry

Figure 1. Larval duration for fall armyworm reared on a check (CK) pinto bean diet, and diets containing silks of Stowell's Evergreen corn (SEG), a susceptible cultivar, and Zapalote Chico corn (ZC), a resistant cultivar. ZC5, ZC10, and ZC20 = 5 g, 10 g, and 20 g of ZC silk in 300 ml of check diet respectively.

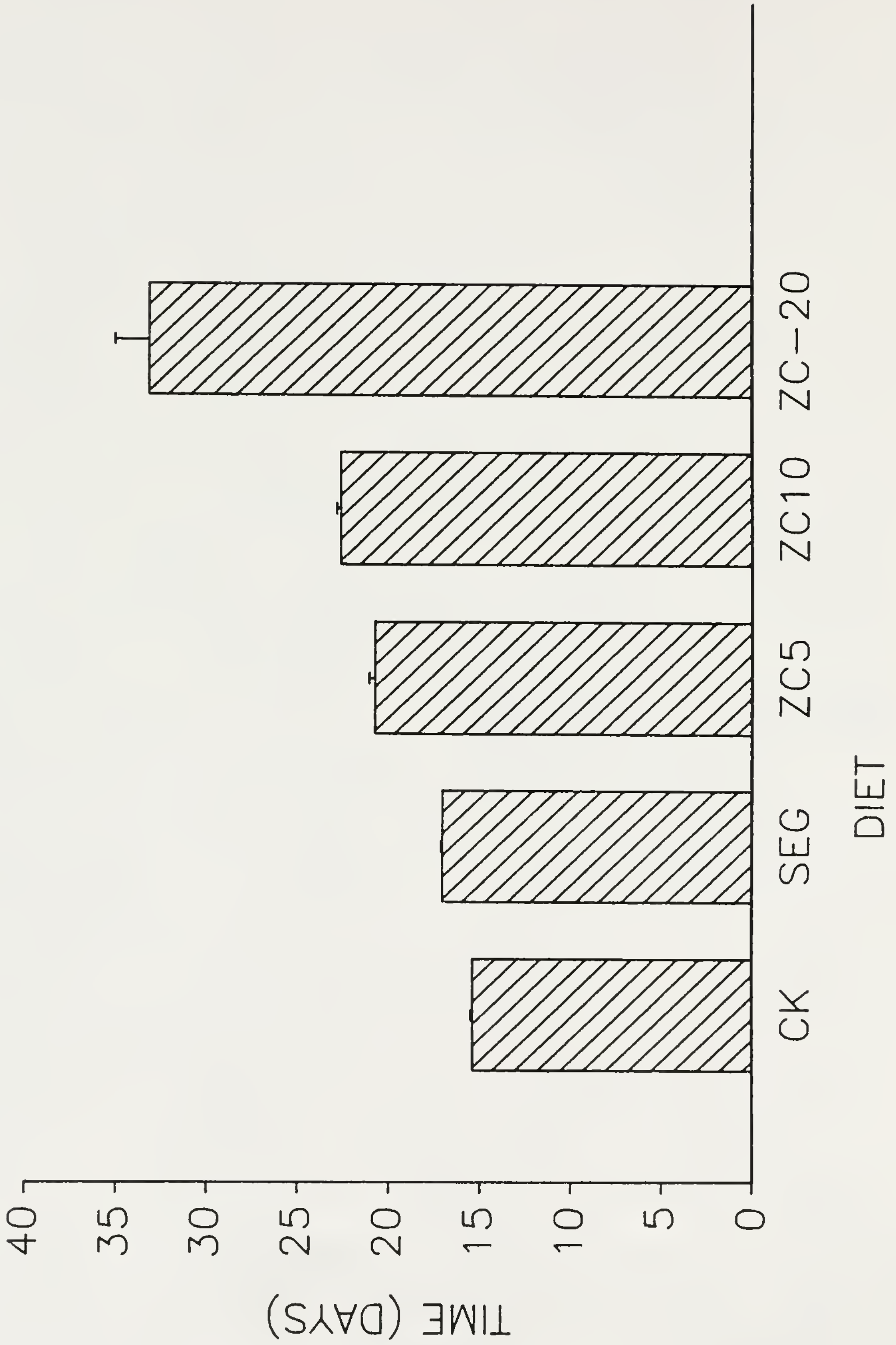

TIME (DAYS)
0
5
10
15
20
25
30
35
40
CK
SEG
ZC5
ZC10
ZC—20
DIET

Figure 2. Developmental time for fall armyworm larval instars 5 to pupation, on diets containing silks of Stowell's Evergreen corn (SEG), a susceptible cultivar, and Zapalote Chico corn (ZC), a resistant cultivar. ZC5, ZC10 and ZC20 = 5 g, 10 g, and 20 g of ZC silk in 300 ml of check diet respectively.

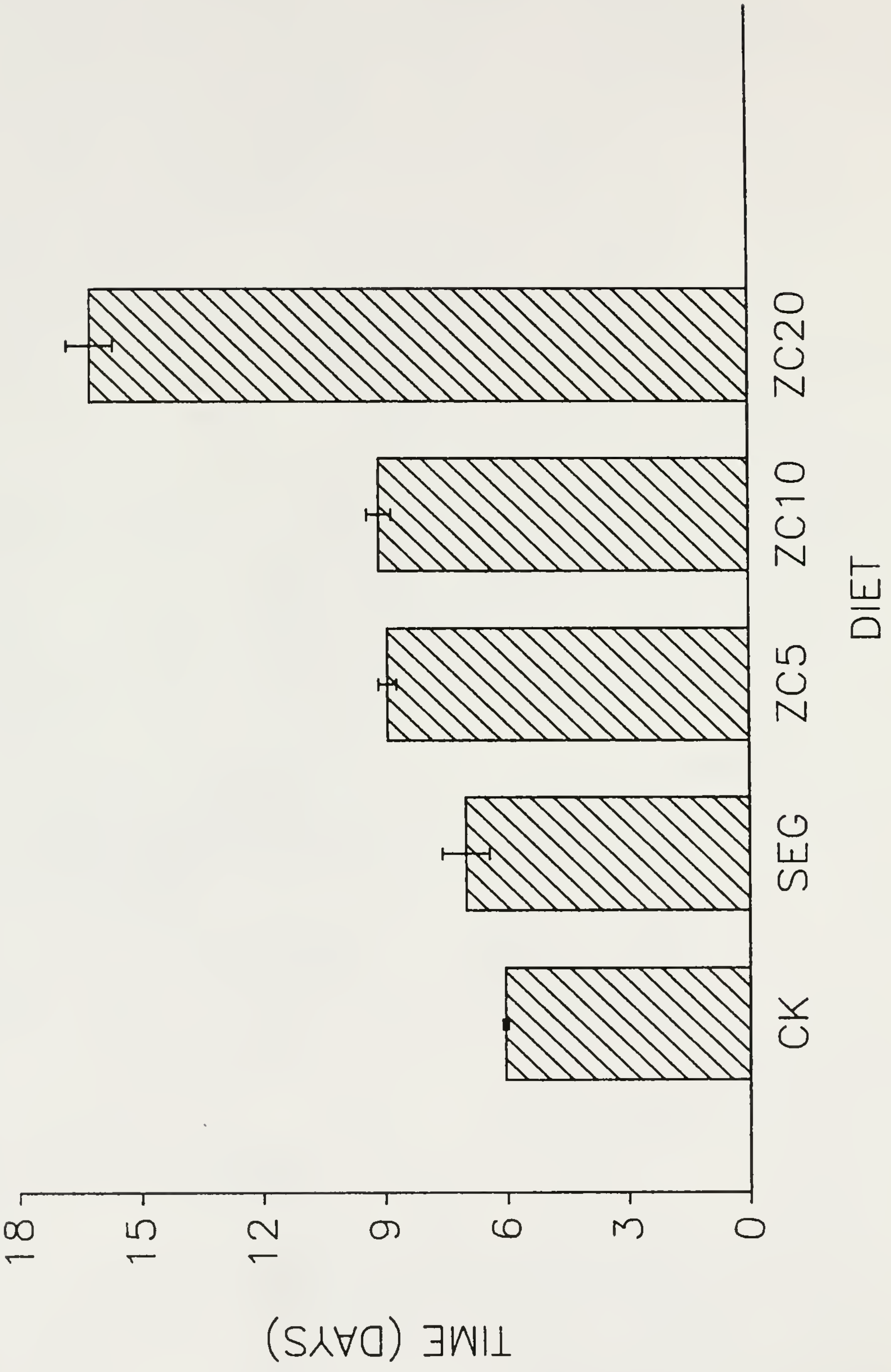

TIME (DAYS)
0
3
6
9
12
15
18
CK
SEG
ZC5
ZC10
ZC20
DIET

Figure 3. Fresh weights (mg) of newly molted fall armyworm 5th instar larvae reared on a check (CK) pinto bean diet, and diets containing silks of Stowell's Evergreen corn (SEG), a susceptible cultivar, and Zapalote Chico corn (ZC), a resistant cultivar. ZC5, ZC10, ZC20 = 5 g, 10 g, 20 g of ZC silk in 300 ml of check diet respectively.

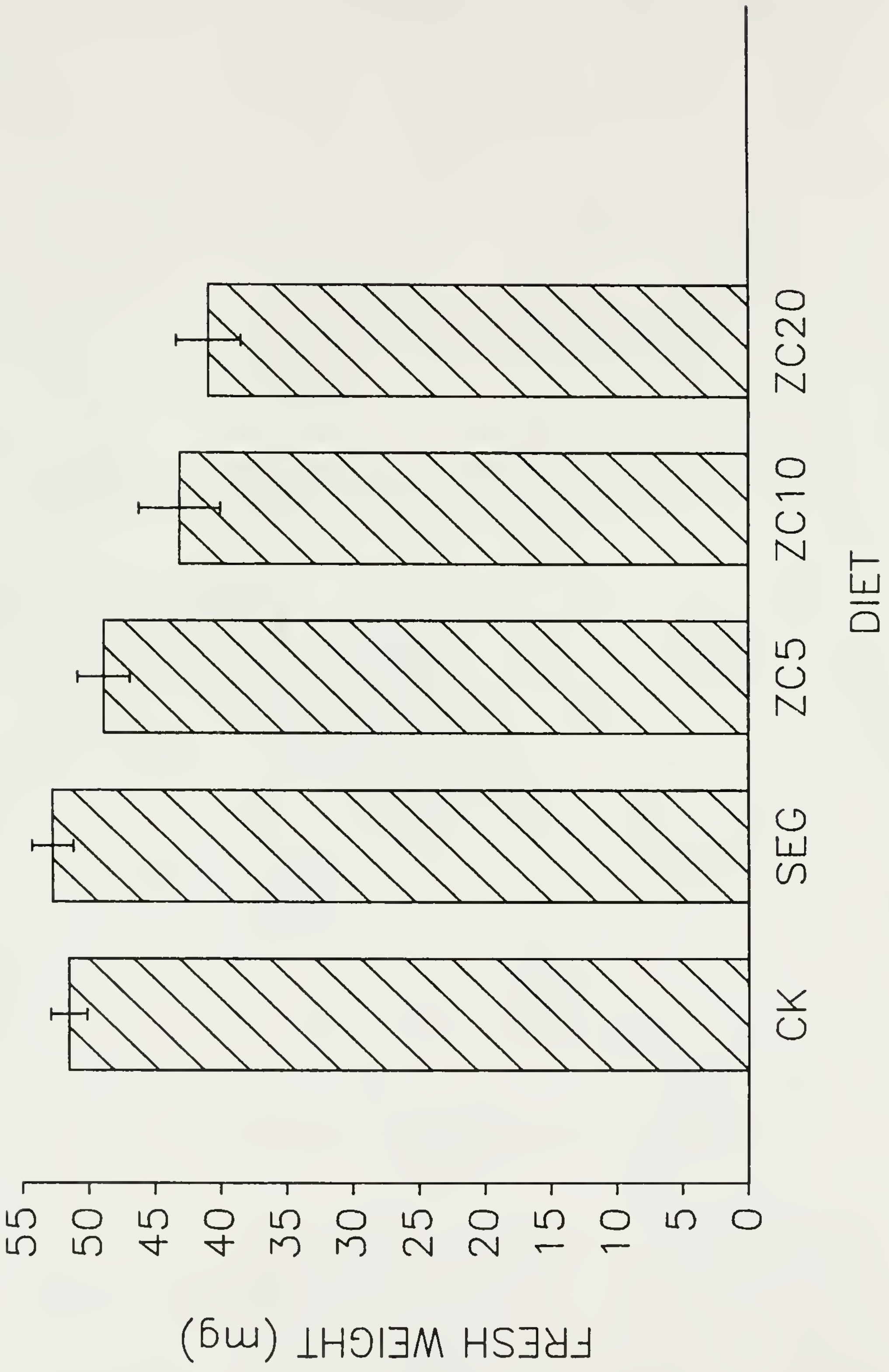
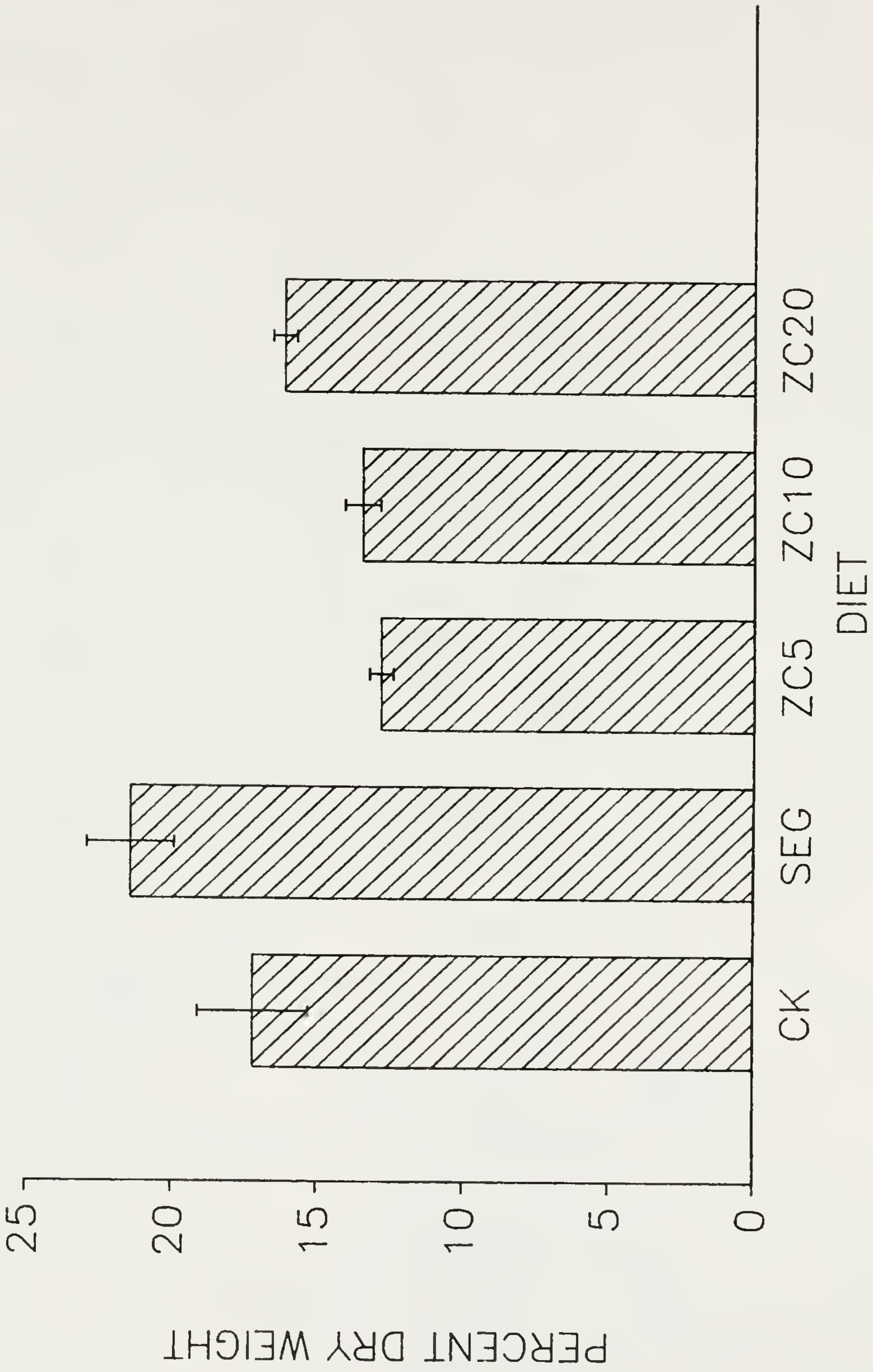

FRESH WEIGHT (mg)
0
5
10
15
20
25
30
35
40
45
50
55
CK
SEG
ZC5
ZC10
ZC20
DIET

Figure 4. Percent dry weight of 5th instar fall armyworm larvae reared on a check (CK) pinto bean diet, and diets containing silks of Stowell's Evergreen corn (SEG), susceptible cultivar, and Zapalote Chico corn (ZC), a resistant cultivar. ZC5, ZC10, and ZC20 = 5 g, 10 g, and 20 g of ZC silk in 300 ml of check diet respectively.


PERCENT DRY WEIGHT
25
20
15
10
5
0
CK
SEG
ZC5
ZC10
ZC20
DIET

weight decreased to a significantly lower weight of 44.20 mg compared to 76.26 mg on the CK diet.

Diet Dry Weights

Significant differences were found among the dry weight percent of the different diets (Figure 7). This may have been due to the quantity of silk in the different diets. The ZC-20 g diet had the highest dry weight content at 38%. The maximum difference in percentage dry weight between diets was 11 percentage points (i.e. 38-27%).

Relative growth rate

The relative growth rate (RGR = RCR x AD x ECD) [biomass dry weight gain (mg)/average caterpillar dry weight (mg)/developmental time (days)] also decreased with an increase of ZC silk in the diet consumed (Table 2). The FAW larvae reared on the ZC-10 g diet had an RGR of 0.26 mg/mg/day while larvae reared on the ZC-20 g silk diet had an RGR of 0.13 mg/mg/day. A doubling of silk concentration in this instance gave rise to a 50% reduction in growth rate. This trend was not observed between ZC-5 and ZC-10.

Relative consumption

The relative consumption rate of dry weight (dw) (RCR = mg dw consumed/mg mean body dw/day) decreased as the silk concentration of Zapalote Chico in the diet increased. The lowest RCR was with the ZC-20 g diet, and the highest on the silk free diet. There was a significant difference in RCR

between the larvae reared on the CK diet and on all the test diets (Table 2).

Approximate Digestibility

There were some significant differences in approximate digestibility (AD = [mg dw consumed - mg dw feces]/mg dw consumed) for larvae feeding on the silk diets, (Table 2). Larvae fed the ZC-5 diet had an AD that was significantly higher than the other diets. The approximate digestibility (AD) estimates the proportion of ingested food (dry weight) that is consumed and assimilated.

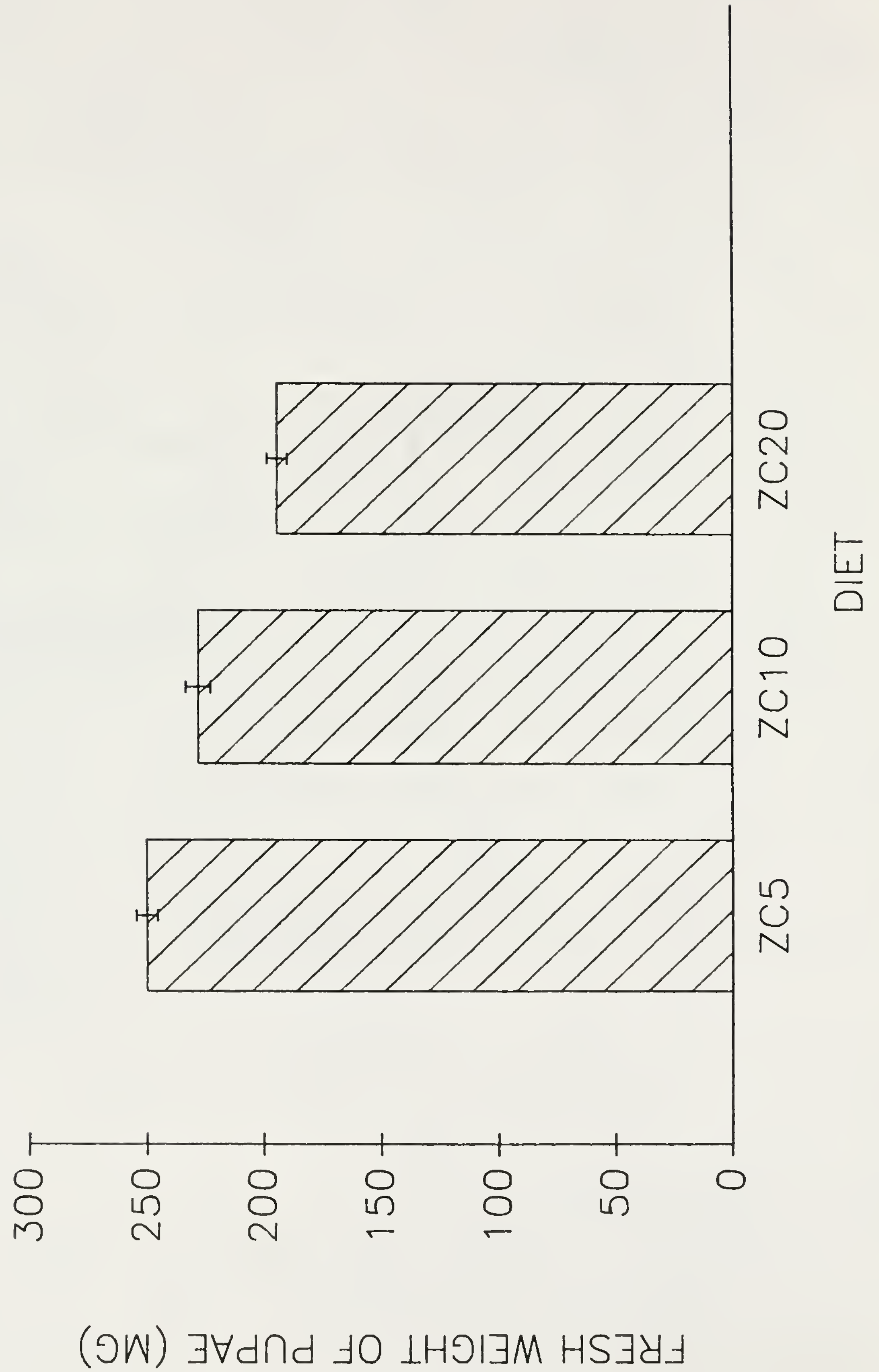
Efficiency of Conversion of Digested Food

Efficiency of conversion of digested food into insect tissue (ECD) [biomass gain/(ingestion-feces) all dry weights] varied significantly on the different diets. No progressive trend was observed with and increase in silk concentration. The ECD for larvae fed the SEG diet was significantly higher than the ECD of for all diets except ZC-10, (Table 2).

Efficiency of Conversion of Ingested Food

The efficiency of conversion of ingested food into insect tissue (ECI) [biomass gain/ingestion, all dry weight mg], decreased on the ZC silk diet. ZC-20, the diet with the highest concentration of silk resulted in the lowest ECI, compared to the highest on the control diet. The ECI

Figure 5. Pupal fresh weights of fall armyworm reared on a pinto bean diet (CK) and diets containing silks of Stowell's Evergreen corn (SEG), a susceptible cultivar, and Zapalote Chico corn (ZC), a resistant cultivar. ZC5, ZC10, and ZC20 = 5 g, 10 g, and 20 g of ZC silk in 300 ml of check diet respectively.



FRESH WEIGHT OF PUPAE (MG)
0
50
100
150
200
250
300
ZC5
ZC10
ZC20
DIET

Figure 6. Pupal dry weights of fall armyworm reared on a meridic pinto bean diet (ck), and diets containing silks of Stowell's Evergreen corn (SEG), a susceptible corn, (S) and Zapalote Chico corn (ZC), a resistant cultivar. ZC5, ZC10, and ZC20 = 5 g, 10 g, and 20 g of ZC silk in 300 ml of check diet respectively.

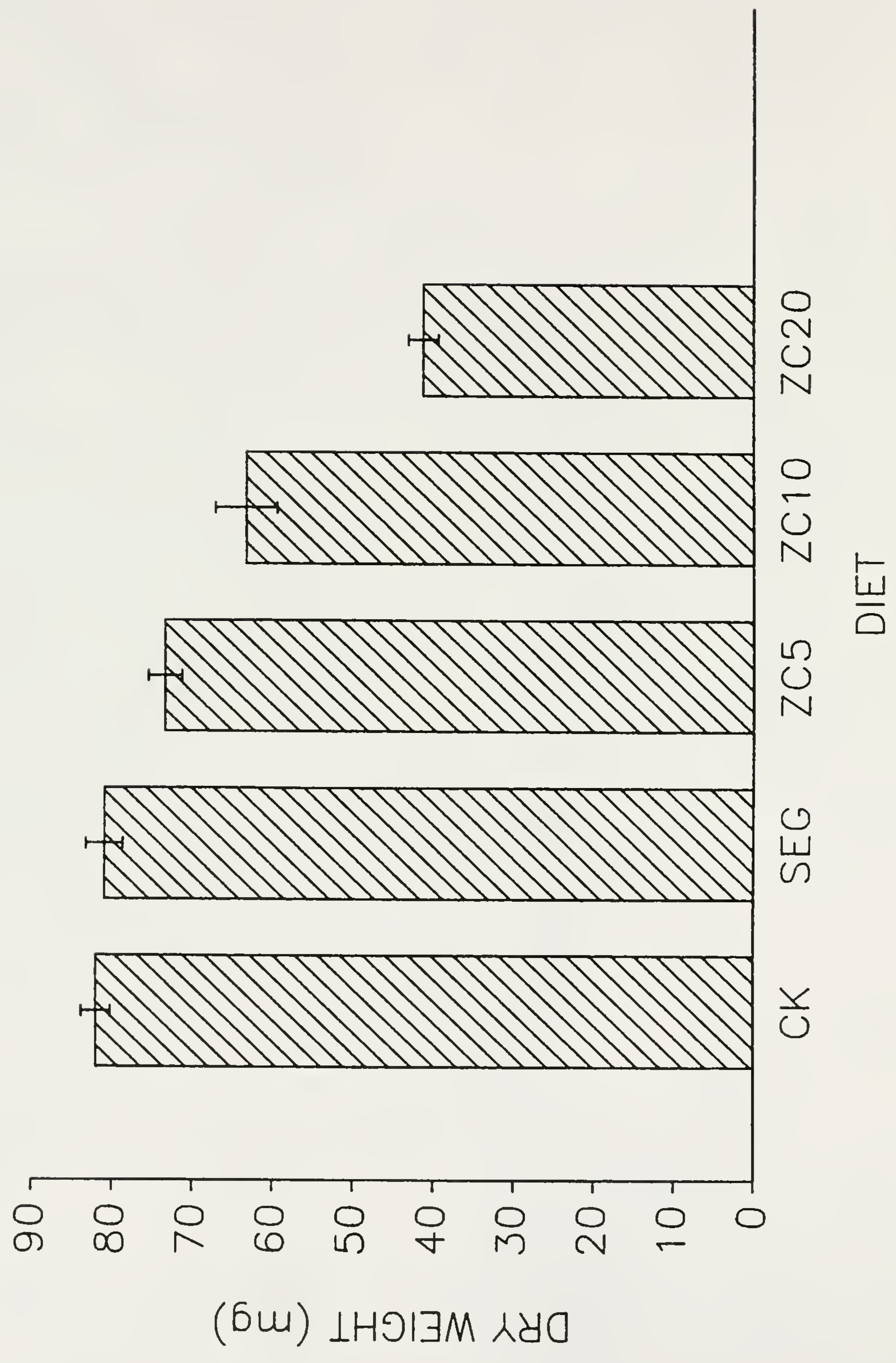

DRY WEIGHT (mg)
0
10
20
30
40
50
60
70
80
90
CK
SEG
ZC5
ZC10
ZC20
DIET

Figure 7. Percentage dry weight of fall armyworm a pinto bean check diets containing silks of Stowell's Evergreen (S) and Zapalote Chico (R) corn. ZC5, ZC10, and ZC20 = 5 g, 10 g and 20 g of ZC silk in 300 ml of check diet respectively.

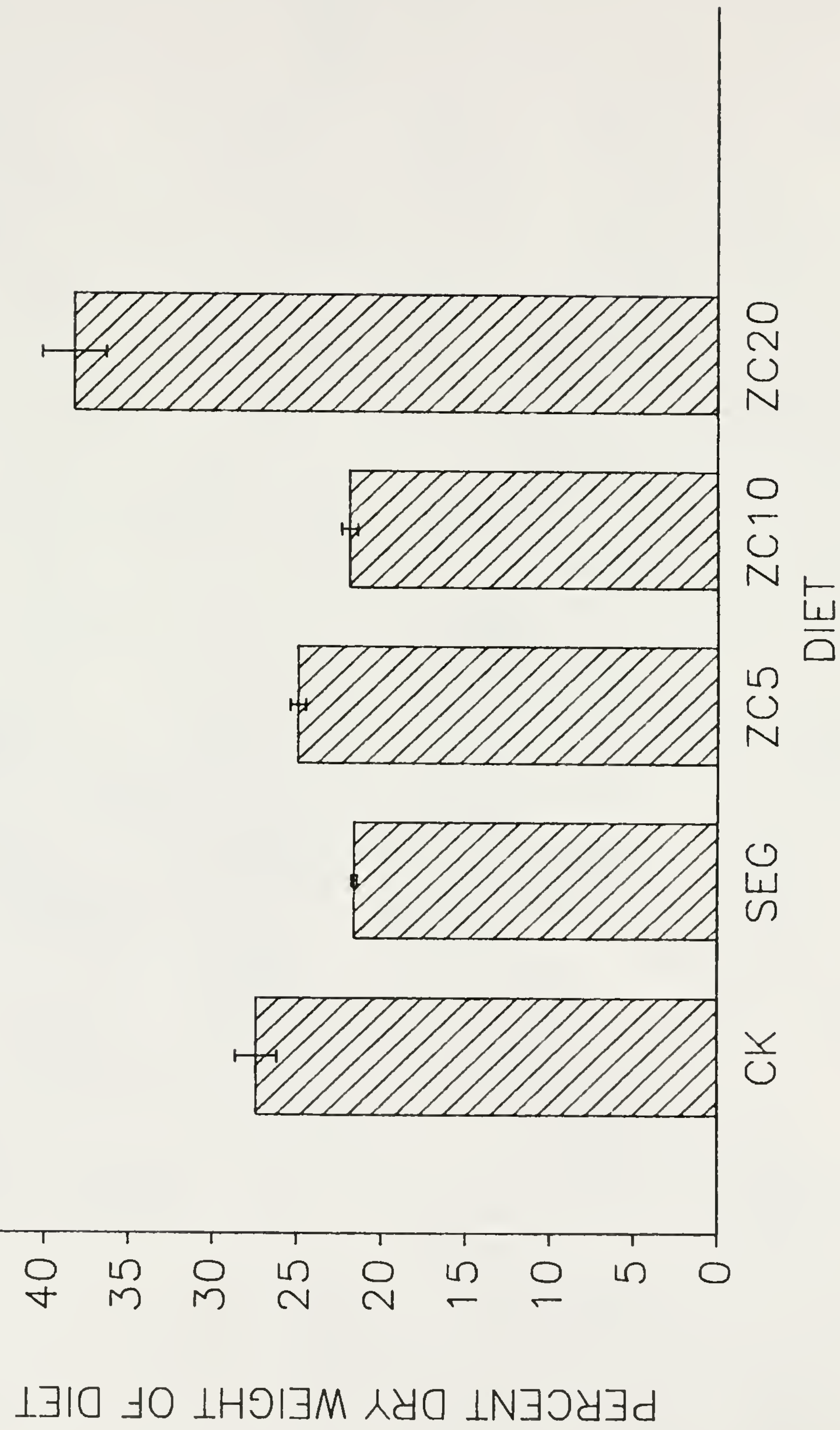
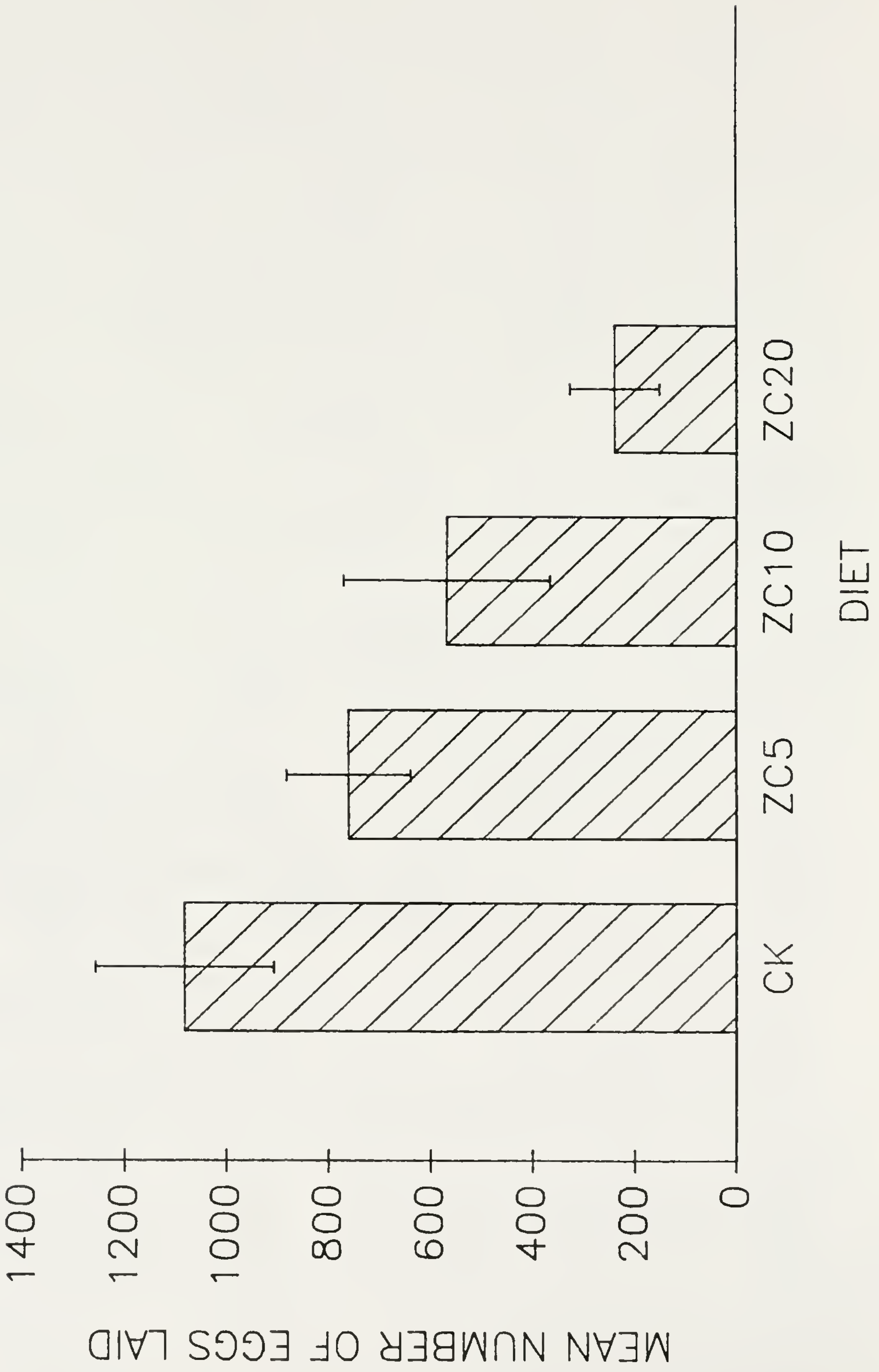

PERCENT DRY WEIGHT OF DIET
0
5
10
15
20
25
30
35
40
45
CK
SEG
ZC5
ZC10
ZC20
DIET

Figure 8. Mean number of eggs laid by fall armyworm females reared on a pinto bean check diet (CK) and diets containing silks of Stowell's Evergreen corn (SEG) a susceptible cultivar, and Zapalote Chico corn (ZC) a resistant cultivar. ZC5, ZC10, and ZC20 = 5 g, 10 g and 20 g of ZC silk in 300 ml of check diet respectively.


MEAN NUMBER OF EGGS LAID
0
200
400
600
800
1000
1200
1400
CK
ZC5
ZC10
ZC20
DIET

for larvae fed the CK, SEG and ZC-10 diets did not differ significantly. FAW larvae feeding on the SEG silk diet had a higher ECI than FAW feeding on the ZC-5 diet.

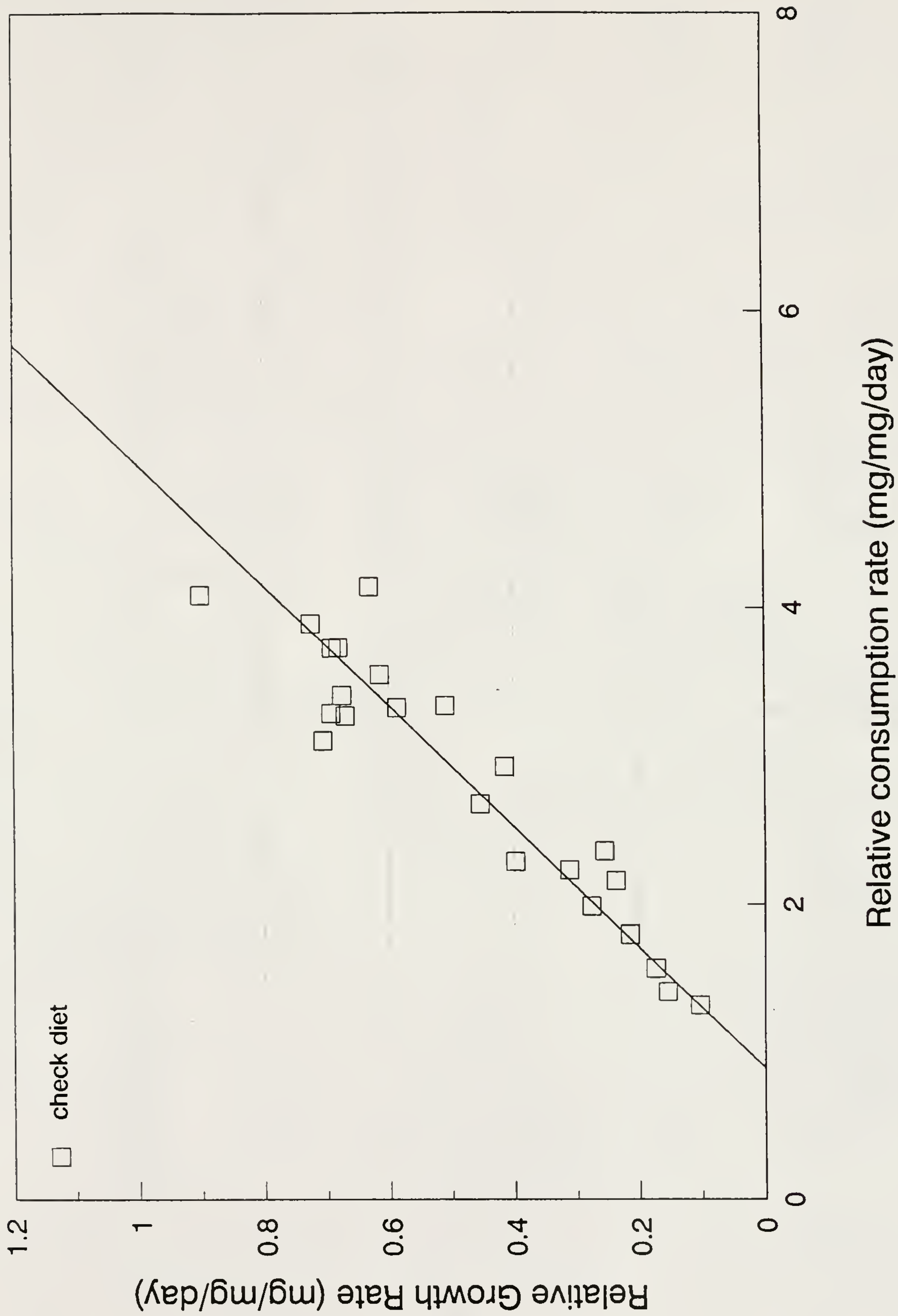
Fecundity

Lynch et al. (1983) described a way of estimating fecundity by using the regression of egg mass weight on number of eggs and larvae to determine the number of eggs per mass and total fecundity of the fall armyworm. The FAW egg mass consists of several layers of eggs, the bottom layer containing the largest number of eggs. Determination of FAW fecundity is, therefore, laborious when eggs are counted individually, but in order to be accurate, this most laborious method was employed. The mean numbers of eggs laid by FAW females reared from 1st instar to pupation on the pinto bean check diet and diets containing silks of ZC are shown in Figure 8. An increase in ZC silk resulted in a decrease in eggs laid. FAW females fed the ZC-20 g diet laid significantly fewer eggs than females reared on the CK and other test diets (Scheffe's test; Table A-3).

Toxicity/Feeding Inhibition Study

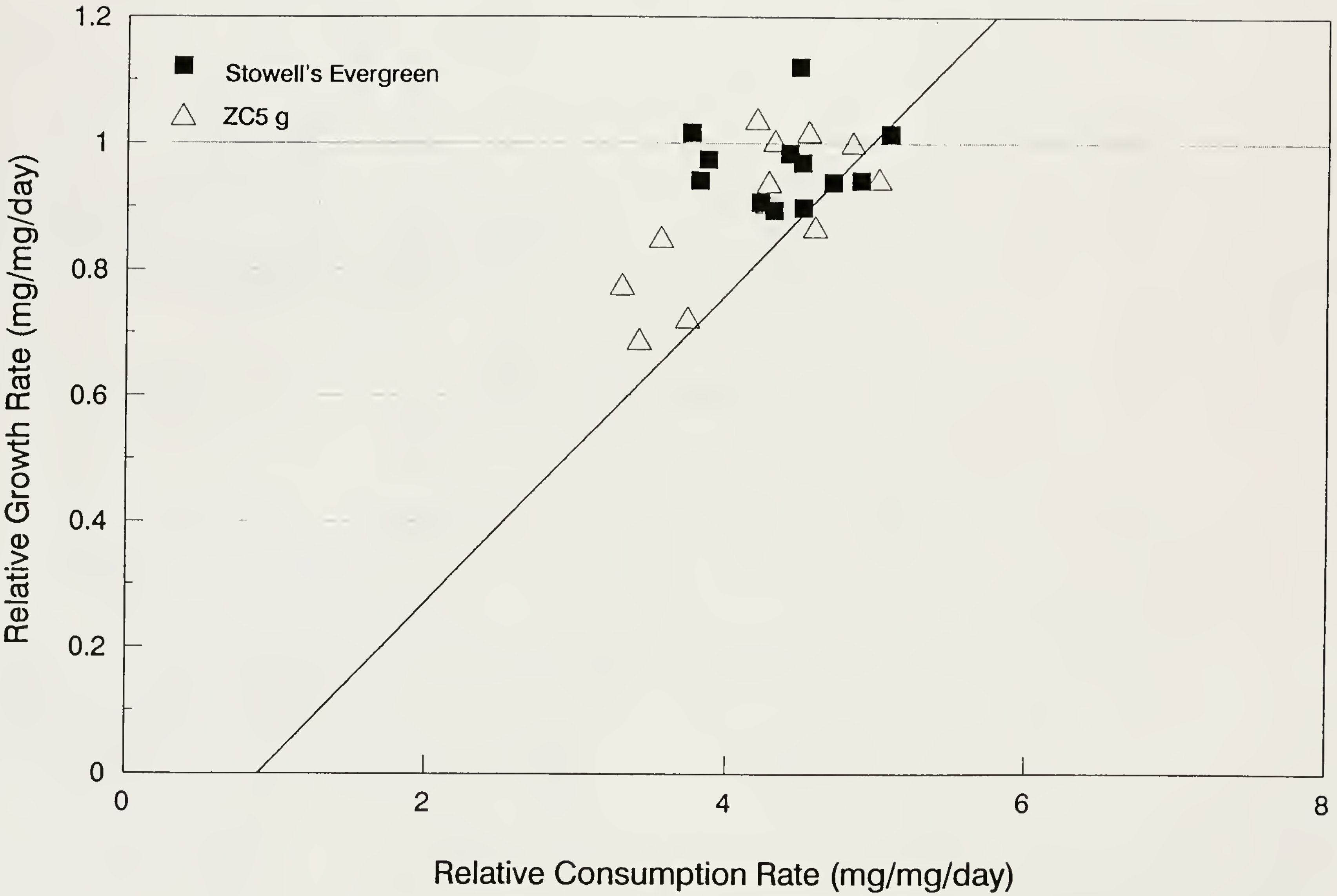
Figure 9 illustrates the estimated regression line for FAW consumption and growth rate when feeding on a pinto bean meridic diet with plots of growth rates against consumption rates for FAW larvae feeding on the check diet (no silks) for 24 hrs.. The r^2 for the regression line was 0.8876.

Figure 9. Calibration curve for 5th instar fall armyworm feeding on a pinto bean check diet. Estimated regression line for relative growth rate (RGR) against relative consumption rate (RCR) for 24 hour feeding.



check diet
Relative Growth Rate (mg/mg/day)
Relative consumption rate (mg/mg/day)
0
0.2
0.4
0.6
0.8
1
1.2
2
4
6
8

Figure 10. Calibration curve for fall armyworm feeding on a meridic diet, with plots of growth rates against consumption rates for larvae feeding on diets containing 5 g each of silks of Stowell's Evergreen and Zapalote Chico corn.


Stowell's Evergreen
ZC5 g
Relative Growth Rate (mg/mg/day)
Relative Consumption Rate (mg/mg/day)
0
0.2
0.4
0.6
0.8
1
1.2
0
2
4
6
8

The equation obtained was:

$$RGR=(RCR \times 0.2458) - 0.2191$$

This is the calibration curve indicating the effect of varying consumption rate on larval growth rate in the absence of corn silks. Figure 10 shows plots of growth rates against consumption rates for FAW larvae feeding on diets containing 5 g of SEG and ZC silks for 24 hrs. These plots are close tothe calibration curve. They are neither below the curve, which would have been indicative of toxicity, nor do they fall in the low consumption range. These diets, SEG and ZC-5 are neither toxic nor do they inhibit feeding. Figure 11 shows plots of growth rates against consumption rates for FAW larvae feeding on diets containing 10 and 20 g of ZC silks for 24 hrs. These points fall below the calibration curve, giving an indication that these diets may prove to be toxic to FAW. If feeding had been inhibited, the points would have fallen on the calibration curves, but in the range of low consumption rate. This leads to the conclusion that the antibiosis resistance observed for Zapalote Chico corn against FAW larvae is a direct result of an antibiotic agent that is toxic to the FAW. Tables 3 and 4 show biomass gained, feeding and growth rates, as well as efficiency parameters for FAW feeding for 24 hrs on the different silk diets. Figure 12 shows all plots of growth rates and consumption

Figure 11. Calibration curve for FAW feeding on a meridic diet, with plots of growth rates against consumption rates for alrvae feeding on diets containing 10 g and 20 g of Zapalote Chico corn silks.

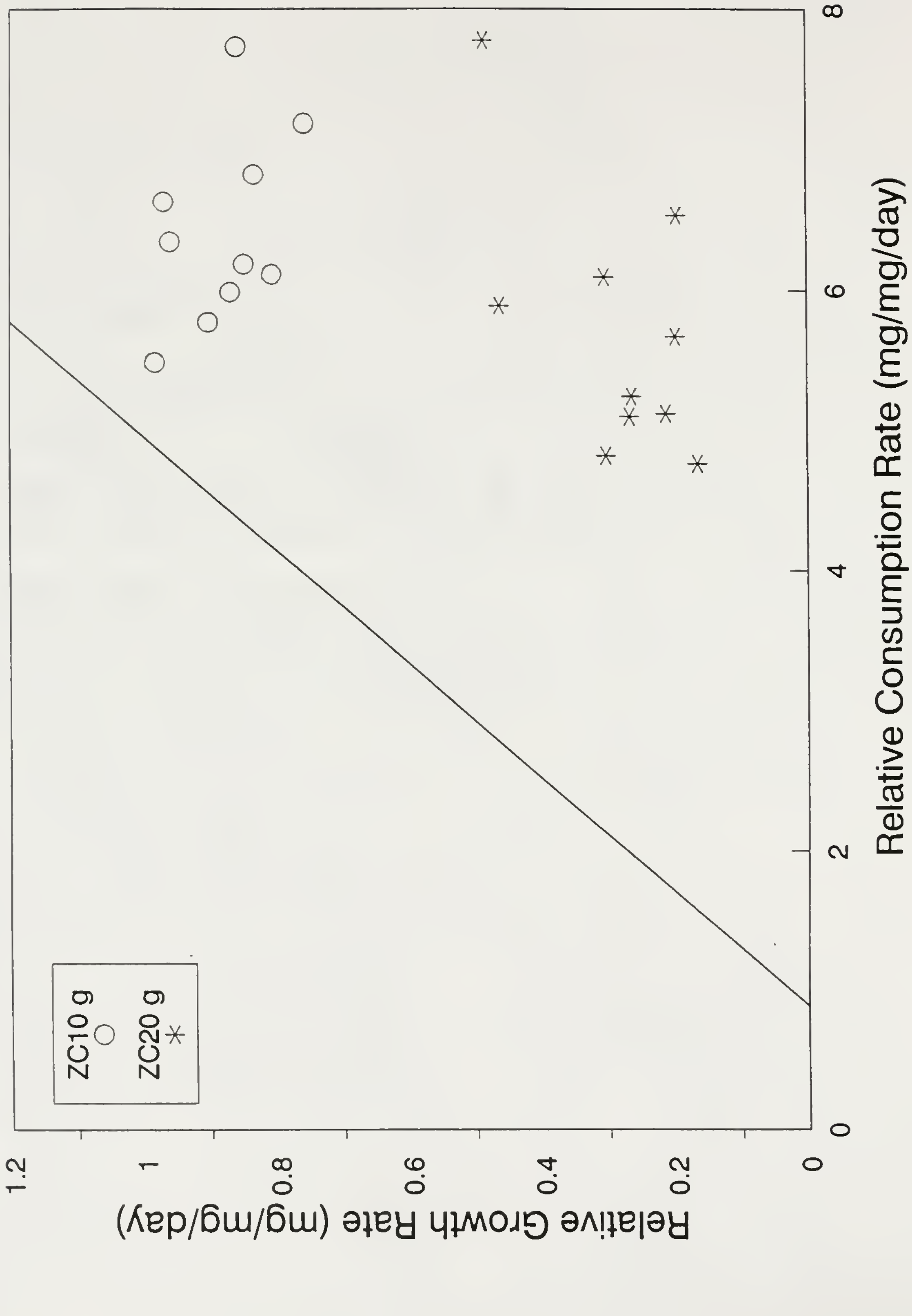
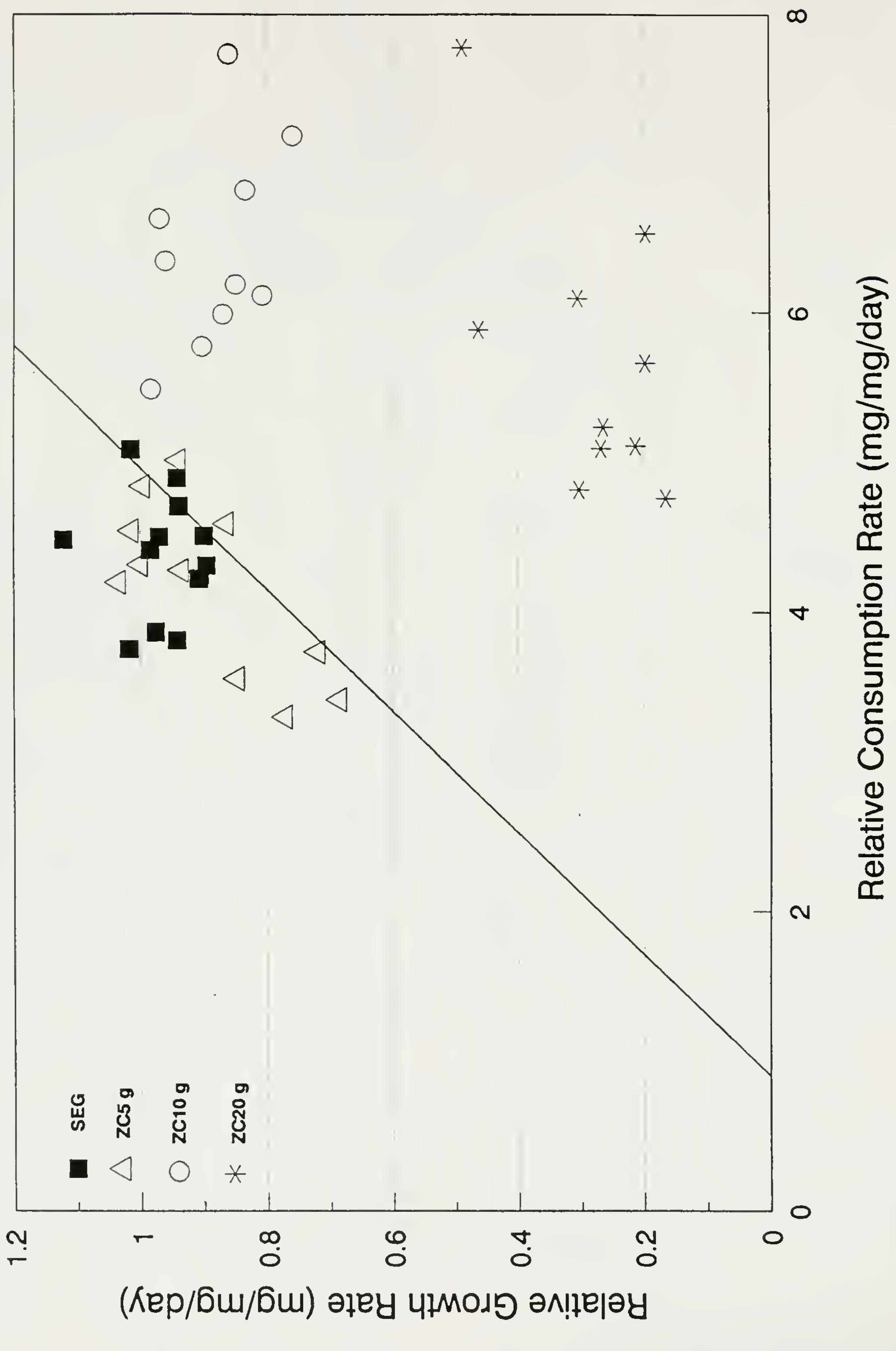

Relative Growth Rate (mg/mg/day)
Relative Consumption Rate (mg/mg/day)
ZC10 g
ZC20 g
0
0.2
0.4
0.6
0.8
1
1.2
0
2
4
6
8

Figure 12. Calibration curve for fall armyworm feeding on a pinto bean check diet, with plots of growth rates (RGR) against consumption rate (RCR) for larvae feeding on test diets containing silks of resistant and susceptible corn cultivars. (5 g of Stowell's Evergreen corn silk and 5 g,10 g, and 20 g of Zapalote Chico corn silks).



SEG
ZC5 g
ZC10 g
ZC20 g
Relative Growth Rate (mg/mg/day)
Relative Consumption Rate (mg/mg/day)
0
0.2
0.4
0.6
0.8
1
1.2
0
2
4
6
8

TABLE 3. Developmental parameters (Consumption, growth and biomass)of 6th instar fall armyworm larvae feeding on diets containing silks of a resistant corn cultivar Zapalote Chico and a susceptible corn cultivar Stowell's Evergreen. (24hrs).

Diet	Developmental Parameters[a]				
	Bi	Bf	B	B	I
Pinto bean (check)	9.10 a (0.58)	22.49 a (0.60)	13.40 a (1.12)	15.79 a (1.07)	82.30 a (3.10)
Stowell's Evergreen	7.05 b (0.21)	20.33 a (0.75)	13.28 a (0.62)	13.69 b (0.46)	59.67 b (1.90)
Zapalote Chico - 5 g	6.53 b (0.26)	17.10 b (0.65)	10.57 b (0.59)	11.82 c (0.40)	49.01 c (2.00)
Zapalote Chico - 10 g	5.39 c (0.30)	13.93 c (0.82)	8.54 b (0.56)	9.66 d (0.55)	63.31 b (1.73)
Zapalote Chico - 20 g	7.62 b (0.53)	10.11 d (0.74)	2.49 c (0.35)	8.86 d (0.62)	52.59 c (2.91)

[a] Measurements expressed in mg dry weight. Values expressed as mean +/- Standard error); in each column, values not followed by the same letters are significantly different ($p < 0.05$; LSD). Parameters defined in Table A-1. All weights in mg. Sample sizes were 9 (check), 12 (SEG), 12 (ZC 5 g), 12 (ZC 10 g), 11 (ZC-20 g).

TABLE 4. Rates of consumption, rates of growth, and efficiency of conversion of ingested food for 6th instar FAW larvae reared on diets containing silks of resistant corn cultivar Zapalote Chico and a susceptible corn cultivar Stowell's Evergreen. (24 hrs).

Diet	Developmental Parameters[a]		
	RCR	RGR	ECI
Pinto bean (check)	5.32 b (0.23)	0.84 b (0.26)	0.16 b (0.01)
Stowell's Evergreen	4.38 c (0.12)	0.97 a (0.18)	0.22 a (0.01)
Zapalote Chico - 5 g	4.17 c (0.16)	0.89 b (0.03)	0.21 a (0.01)
Zapalote Chico - 10 g	6.71 a (0.27)	0.88 b (0.02)	0.13 c (0.01)
Zapalote Chico - 20 g	6.18 a (0.55)	0.28 c (0.03)	0.05 d (0.01)

[a] Parameters defined in Table A-1. Values expressed as mean (+/- standard error); in each column, values not followed by the same letter are significantly different ($p < 0.05$; LSD). All weights in mg. Sample sizes were 9 (check), 12 (SEG), 12 (ZC-5 g), 12 (ZC-10 g), 11 (ZC-20 g).

rates for all the test diets, plotted against the calibration curve.

General Discussion

Using the method of Blau et al. 1978, the mechanism of resistance of Zapalote Chico corn was determined to be one of antibiosis resulting from toxicity. This supports observations made by Wiseman and Widstrom (1986) on the mechanisms of resistance in Zapalote Chico corn silks to FAW larvae, but further specifies the basis of antibiosis observed. The toxic effect of ZC corn silks may explain some results obtained for FAW developmental parameters measured during the 5th and 6th instars for FAW reared on control check and silk diets such as reduced final body weight (Bf), reduced relative growth rate (RGR), reduced relative consumption rate (RCR).

Increased food consumption in response to reduced nutrient levels is well documented (Slansky and Wheeler 1989; Scriber and Feeny 1979; Timmins et al., 1988). However increasing the quantity of an allelochemical or toxin as occurred here warrants a different set of responses. Allelochemicals have been implicated as factors responsible for reduced feeding rates and efficiencies (Slansky and Scriber 1985), and for inhibiting and prolonging insect growth (Stipanovic 1983). There was no

significant difference in body weight attained by the 5th instar (Bi) by larvae reared on the check and ZC silk diets. However final body weight (Bf), biomass gained (B) and mean body weight (MB) decreased with an increase in ZC silk. Over the fifth and sixth instar, the decline in biomass gained (B) with increase in ZC silk was directly associated with the decrease in food consumption (I), RCR, RGR, and ECI. The toxicity of the ZC silk may have been the cause of mortality observed in larvae fed the ZC-20 g diet.

The increase in percentage dry weight of the ZC-20 g diet may have been responsible for the decline in consumption rate, and may have been a confounding factor in the interpretation of a xenobiotic causing the decline in consumption rate. There was no progressive increase in percentage dry weights of the Z. Chico silk diets that can be directly correlated to the progressive decrease in consumption rate observed with an increase in Z. Chico silk concentration.

Pupal weight and fecundity declined significantly as ZC silk content of FAW diet increased. This is an indication of an inability to fully compensate for the effects of the toxicity of the xenobiotic in the silks of ZC. This reduction in fecundity will have ecological consequences. Reduced fecundity in one generation implies a decrease in population size of the subsequent generation. Increased mortality in the larval stage has similar consequences. In the context of pest management, this is an ideal situation,

as reduction in FAW populations would greatly reduce crop damage and alleviate movement to alternate crops.

Prolonged developmental time makes larvae vulnerable to a number of mortality agents for a longer period e.g. parasites and predators (Price et al., 1980). The resistant variety may have effects on natural enemies of herbivores that are indirect in nature. A study of the effects a resistant corn cultivar has on an economically important pest such as the FAW, results in a better understanding of interactions between the pest and host plant. Toxic compounds in plants can be sequestered or cycled in herbivores and used as defenses against the third trophic level (Price 1986). Toxic compounds and allelochemicals have an effect on the detoxication enzymes of FAW (Yu 1982). The detoxication enzymes may be stimulated or induced, increasing or decreasing the insects ability to detoxify other xenobiotics such as pesticides. Understanding the mechanisms of a resistant corn cultivar at the biochemical level would constitute useful information that could be utilized in the design of pest control strategies.

CHAPTER III

FIELD PERFORMANCE OF *ARCHYTAS MARMORATUS* AGAINST FALL ARMYWORM *SPODOPTERA FRUGIPERDA* ON STOWELL'S EVERGREEN, A SUSCEPTIBLE CORN CULTIVAR AND MpSWCB-4 A RESISTANT CORN CULTIVAR

Luginbill (1969), among others, considers the use of resistant varieties an ideal method for controlling insects. A fundamental requisite for development of IPM strategies in corn is a precise understanding of the relationships between corn genotypes and beneficial insects. It is important to understand the relationships among host larvae, their diets, and natural enemies, to determine the effectiveness of these natural enemies as biological control agents.

Resistant varieties and natural biological control agents may ultimately prove invaluable in developing management programs for corn pests. Resistant varieties may enhance natural control organisms, because insects feeding on resistant plants generally require more time for development and may be in a weakened condition (Maxwell et al. 1972, Turnipseed and Sullivan 1976). Information on the influence of resistant corn varieties upon beneficial insect populations is lacking. Isenhour et al. (1989a) researched enhanced predation by the bug *Orius insidiosus* (Say) on larvae of *Helicoverpa zea* (Boddie) and *Spodoptera frugiperda*

(J.E.Smith) (FAW) caused by prey feeding on a resistant corn genotype "MpSWCB-4". FAW larvae fed the resistant MpSWCB-4 had significantly higher rates of predation by adult O. insidiosus than did armyworm fed "Cacahuancintle", a susceptible genotype. Studies on the European corn borer, Ostrinia nubilalis (Hübner), and a tachinid parasitoid, Lydella grisescens Robineau-Desvoidy indicated that corn variety influenced the rate of parasitization (Franklin and Holdaway 1966). In cotton, glabrous phenotypes are less attractive to H. zea for oviposition than are hirsute phenotypes; however, rates of egg parasitization by Trichogramma pretiosum (Riley) were greater in glabrous types (Treacy et al. 1985). On the other hand, resistant host plants may be indirectly detrimental to parasitoids by modifying the rate of reproduction and nutrition of developing host larvae (Powell and Lambert 1984, Orr and Boethel 1985).

Parasites, predators and parasitoids represent three different carnivorous, interspecific interactions between animals. In the parasites, many generations may occur on or in a host, and there is a tendency towards the evolution of host specificity and a more complex interrelationship. Predators, on the other hand must locate a large number of prey (= host) in order to grow and reproduce. Parasitoids fall between these two extremes. Only one generation is produced per host, and only the immature stage is parasitic,

while the adults are free living. A parasitoid requires the entire host and kills it, thus eliminating the potential for the evolution of a mutualistic relationship after the host has been attacked. The host becomes a container for the developing parasitoid, enabling the parasitoid to modify the host behavior for its benefit.

The term "parasitoid" was first used by Reuter in 1913 (Hassel and Waage, 1984) to describe insects that develop as larvae on the tissues of other arthropods, which they eventually kill. Parasitoids have been described as "predator-like" parasites.

Fall armyworm is attacked by a diverse complex of natural enemies including 53 known species of parasitoids (Ashley 1979, Gardener and Fuxa 1980). Several laboratory studies have been carried out to assess the effectiveness of selected parasitoids as biotic control agents of FAW (Mitchell et al. 1984, Isenhour 1985, Pair et al. 1986a).

Archytas marmoratus (Townsend) is a tachinid parasitoid (larval-pupal) of the Noctuidae in North and South America and in the West Indies (Sabrosky 1978, Ashley 1979). Numerous authors have reported its occurrence throughout the southern United States (Quaintance and Brues 1905, Luginbill 1928, Vickery 1929, Bibby 1942, Parencia 1964, Shepard and Sterling 1972). Findings by Gross et al. (1976) from collections of 5th and 6th-instar larvae of *H. zea* and *S. frugiperda*, respectively, on corn indicated that *A. marmoratus* is a major parasitoid of these species,

particularly in south Georgia and north Florida.

Gross and Johnson (1985) discussed advances in large-scale rearing and biological studies of A. marmoratus. Gross et al. (1985) evaluated the performance of mechanically extracted maggots of A. marmoratus against larval populations of H. zea and FAW on whorl and tassel-stage corn.

Evaluating the effects of a variety of corn on a parasitoid of fall armyworm represents a tri-trophic interaction, with corn as the producer, fall armyworm the primary consumer and the parasitoid a secondary consumer. Insect parasitoid-host relationships are often considered to be simple, and compatibility of a parasitoid as a control method with resistant varieties has been assumed.

Figure 13 illustrates interactions that occur in three trophic levels. Price (1986) describes two kinds of plant defense or plant resistance: INTRINSIC DEFENSE, where the plant alone produces the defense through production of chemicals such as toxins or digestibility reducers, or through physical defense by trichomes or toughness and EXTRINSIC DEFENSE of plants, when the plant benefits from the natural or applied enemies of herbivores. He states that plant breeders have emphasized the study of intrinsic defense mechanisms; whereas, those studying biological control of herbivores have emphasized the need for extrinsic defense of plants. A dichotomy results because each of the

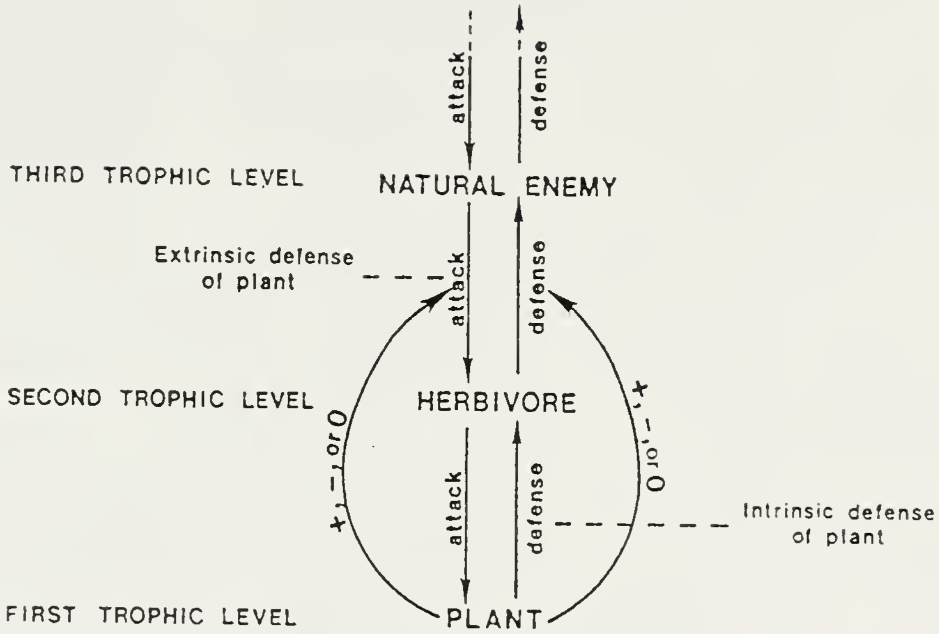


Figure 13. The kinds of interactions, direct and indirect, in a typical food web, showing the relationships between intrinsic and extrinsic defense of plants and the trade-offs between them. +, −, 0 indicate positive, negative or noeffects, the plants may impact on the herbivore-natural enemy relaionship. From Price (1986).

above mentioned independent disciplines is interested in two trophic level systems. The two groups appear to be melding at present and, during the last decade, the details of direct and indirect effects of plants on herbivores and their natural enemies at the chemical level are receiving much attention (e.g. Bergman and Tingey 1979, Bell and Carde 1984, Barbosa and Letourneau 1988).

Host diet influences suitability of a host for a parasitoid. Slansky (1986) discussed the nutritional ecology of endoparasitic insects and their hosts. Campbell and Duffey (1979) described a case of potential incompatibility of plant antibiosis with biological control. Effects of pest-resistant soybeans on the development of hymenopterous parasitoids of Lepidoptera have been studied (Yanes and Boethel, 1983; Powell and Lambert, 1984; Orr and Boethel, 1985; and Beach and Todd, 1986). Rogers and Sullivan (1986) studied the effects of two plant introductions (PIs) on the lygaeid predator _Geocoris punctipes_ (Say). All of these except Slansky (1986) (where nutritional ecology is discussed), document some adverse effects on the development of beneficial species when hosts or prey fed on pest resistant soybean genotypes.

A host may be suitable when feeding on one plant species, but not another. The parasitoid _Hyposoter exiguae_ (Viereck) could not survive in _H. zea_ larvae fed on artificial diet containing even small amounts of the alkaloid α-tomatine, but if cholesterol was added to the

diet, this deleterious effect was eliminated (Greaney et al. 1984). Bergman and Tingey (1979) reviewed various types of interactions that occur between host plants, insect pests, and their natural enemies. There is a direct influence of plant hosts on natural enemies; volatiles, plant growth characteristics, toxic and nutritional factors, and foliage morphology all directly affect natural enemies. Doutt (1964) discussed the directed orientation of predators and parasites to host plants of their prey and the differential attraction that occurs among crop varieties. Franklin and Holdaway (1966) reported differential attraction of *Lydella grisescens* Robineau-Desvoidy, a parasite of the European corn borer, *Ostrinia nubilalis* (Hübner) to different maize hybrids. Many predators and parasites use plant juices, nectar, and pollen as sources of food and water. *O. insidiosus* a predator of *H. zea*, consumes juices and pollen of corn and cotton (Dicke and Jarvis 1962).

Bergman and Tingey (1979) also pointed out that the nutritional substrate offered by a host plant can indirectly influence predator and parasite fitness in several ways; prey confined to resistant hosts commonly experience reduced growth rates, greater developmental time and mortality, and decreased fecundity. Such dramatic alterations of physiological processes may change the nutritional quality of the prey as food/host for predators and parasites.

Gross and Pair (1986) reviewed the impact of endemic parasitoids and predators as regulators of fall armyworm

populations and identified areas of research and development that must be addressed before significant advances can be made in importation and augmentation. Pair et al. (1986) discussed the influence of four corn cultivars on FAW establishment and parasitization. Gross (1988) studied field survival and performance of mechanically extracted maggots of A. marmoratus on FAW and indicated that good field survival occurred.

Isenhour and Wiseman (1988) reported effects of parasitism of the FAW by Campoletis sonorensis (Cameron) as affected by host feeding on resistant Zea mays L. cv. Zapalote Chico. The research described in this chapter examined the use of mechanically extracted larvae of A. marmoratus (Townsend), as a biological control agent against FAW, is compatible with the use of a leaf-feeding resistant cultivar of corn (MpSWCB-4).

Materials and Methods

Two varieties of corn, "Stowell's Evergreen" (SEG) and MpSWCB-4 were planted on an experimental farm near Tifton, Georgia and maintained according to recommended cultural practices. Test plots (2 each year) were planted in May 1988 and 1989. There were ten replicates for each cultivar. Each replicate contained paired rows of each cultivar. Plants in test plot 1 were used for the A. marmoratus performance study, by apply FAW neonate larvae to whorls of

the plants when they reached the 6-8 leaf stage. Plants in test plot 2 were used at the 10-12 leaf stage.

The A. marmoratus (AM) colony used in the study was maintained at the USDA Biology and Population Management Research Laboratory. It had been established in 1981 from fifth-instar CEW larvae occurring in mid-green tassel stages of "Silver Queen" sweet corn near Tifton, Georgia, USA. Additional AM adults, eclosing from pupae of CEW and FAW that were collected in southern Georgia and northern Florida, had been added intermittently to the culture. Laboratory cultures were maintained on CEW larvae from the Tifton laboratory colony (Young et al. 1976) reared by the method of Burton (1969) on corn-soy-milk-solid diet (Burton 1970). AM adults were held in plyboard and screened cages as described by Gross and Young (1984). They were provided with sugar cubes and free water from saturated paper towels in a 1.5 by 10 cm Petri dish during the 10 day pre-larviposition period. A. marmoratus maggots were extracted mechanically from fecund females as described by Gross and Johnson (1985) and suspended in the desired volume of a 0.35% solution of hydroxyethylcellulose (Minidrift) (Soilserv, Inc., Salinas, California.

The FAW larvae were also obtained from a colony maintained at the USDA Biology and Population Management Research Laboratory in Tifton, Georgia. Corn plants at the 6-8 and 10-12 leaf stage were used. Neonate FAW were applied directly into the whorl using a mechanical larval

dispenser developed by Wiseman (Wiseman et al. 1980). FAW eggs deposited on paper towels were placed in plastic bags and held at 32°C until hatch. Larvae were removed by inverting the bags and gently shaking the towel while it remained in the bag, to dislodge larvae. Corn-cob grits (grits-o'cobs No. 2040, Anderson's Cob Division, Maumee, Ohio 43537) were mixed with the FAW larvae in a concentrated form. The FAW-corn cob grits mixture was shaken and diluted until about 20 FAW larvae per delivery were obtained. They were then transported to the field for immediate dispensing into the whorls.

All plants in both the 6-8 and 10-12 leaf stage of both MpSWCB-4 and SEG were infested at the same time. The FAW-grits mixture in the dispensing bottle was thoroughly mixed and repeatedly agitated during the application process to ensure standardized delivery of about 20 FAW neonates per plant. Infestations were made in the morning, after most of the dew had evaporated (ca. 9:00 am).

After 10 days, freshly prepared AM maggots in a mini drift suspension were diluted until an eye dropper delivered larvae at the rate of 25 larvae per drop. One drop of the maggot suspension was applied directly into the centers of the whorls of plants in each "test row" for each replicate, 12 plants per row, 10 replicates per variety. Host larvae (FAW) within the whorl were exposed to AM maggots for 72 hrs, then the FAW were retrieved. The second row of each replicate for each cultivar was left for rating leaf damage

at 14 days. Thirty FAW larvae were collected from each replicate (1 tray) and placed individually on a modified pinto bean diet in 30 ml plastic diet cups. Control FAW larvae were obtained by harvesting 2 plants for each (AM) untreated row of each replicate.

Larvae collected from the field were placed in Percival Growth Chambers at 26.0 ± 1° C, 14:10 L:D photoperiod, and 85 ± 5% RH. Emergence of FAW and all parasites was noted, and percent parasitization calculated. Data were analyzed by PROC GLM (SAS) and percentage parasitization values were changed via arcsin transformation prior to analyses (SAS Institute 1989). Scheffe's method was used (p=0.05) to separate means (SAS Institute 1989). This method of separating means is considered to be conservative, and was selected for that reason.

Results and Discussion

Table 5 lists parasites reared from fall armyworm larvae collected from Stowell's Evergreen and MpSWCB-4 corn in Tifton, Georgia during the month of June in 1988 and 1989. The tachinid *A. marmoratus* was applied after mechanical extraction from fecund females, at the rate of 25 larvae per plant but all other parasites emerging from the FAW larvae represent natural infestations.

In 1988, the naturally occurring ichneumonid parasitoid *Ophion flavidus* Brulle occurred at much higher rates of parasitization of FAW, than the artificially applied

TABLE 5. Parasites reared from fall armyworm larvae collected in Tifton, Georgia, June 1988 and June 1989.

HOST PLANT: Corn

VARIETIES: Stowell's Evergreen and MpSWCB-4

Braconidae
- *Apanteles* sp.
- *Cotesia marginiventris* (Cresson)
- *Rogas laphygmae* Viereck

Eulophidae
- *Euplectrus comstockii* Howard

Ichneumonidae
- *Ophion flavidus* Brulle

Tachinidae
- *Archytas marmoratus* Townsend

parasitoid _A_. _marmoratus_, (Figure 14). There were higher rates of parasitization by AM on the resistant variety (MpSWCB-4) than on the susceptible variety SEG, on both plots, but the differences were not statistically significant (p= 0.05). This trend was reversed with _Ophion_, which had significantly higher rates of parasitization on the susceptible variety than on the resistant. It has been suggested that _Ophion_ may be in direct competition with _Archytas_ in the field (Gross, 1988). In addition, the FAW may have been in the more desired developmental stage for the maggots on the SEG than those on MpSWCB-4 since MpSWCB-4 causes a reduction in growth and development of FAW. There were no significant differences between MpSWCB-4 and SEG at the 6-8 leaf stage, when the total number of larvae parasitized were analyzed. At the 10-12 leaf stage, however, the differences were significant, and the trend of parasite occurrence was higher overall on the susceptible cultivar. _Ophion_ _flavidus_ numbers were higher in the susceptible cultivar and contributed to making overall parasitization rates in 1988 highest in SEG (S), (Figure 14).

Ophion _flavidus_ parasitized 20% of FAW larvae collected from SEG at the 10-12 leaf stage. This was the highest rate of parasitism found in 1988 for a single parasitoid of FAW larvae in the study. _Archytas_ _marmoratus_ had a high of 8%. The highest total percentage parasitism was 31%. This represented parasitization that occurred for only 3 days,

while FAW in the whorl had been exposed to parasitization by other naturally occurring parasites prior to the application of AM.

Figure 15 shows the percentage of total parasitization by the parasitoids in the 1988 field study. *Ophion flavidus* was responsible for as much as 73% of total parasitization, and this occurred at the 10-12 leaf stage on SEG, while the maximum contribution to total parasitization by AM was 37% which occurred in plot 2, on MpSWCB-4. Other parasites, namely *Cotesia marginiventris* (Cresson), *Rogas laphygmae* Viereck, and *Apanteles* sp. together were responsible for as much as 30% of parasitism at the 6-8 leaf stage on both SEG and MpSWCB-4.

In 1989, *Ophion* was less prevalent than in 1988, (Figure 16). Levels of parasitization by AM were higher perhaps due to reduced competition by the absence of *Ophion*. Parasitization by AM was highest on the 10-12 leaf stage of SEG, and lowest on SEG at the 6-8 leaf stage. The trends observed in 1988, with higher levels of parasitism on MpSWCB-4 were not consistent in 1989. AM did significantly better at the 6-8 leaf stage on MpSWCB-4 than on SEG, parasitizing 13% and 8%, respectively, of FAW larvae. At the 10-12 leaf stage, AM did better on SEG but not significantly better.

A. marmoratus was responsible for over 95% of total parasitism found on SEG at both stages of plant development and 65-80% of parasitism on MpSWCB-4, Figure 17. The

Figure 14. Percentage parasitization by artificially applied _Archytas mormoratus_, _Ophion flavidus_ and other parasites, of fall armyworm collected from a susceptible corn cultivar, Stowell's Evergreen and a resistant corn cultivar MpSWCB-4 in Tifton, Georgia, 1988.

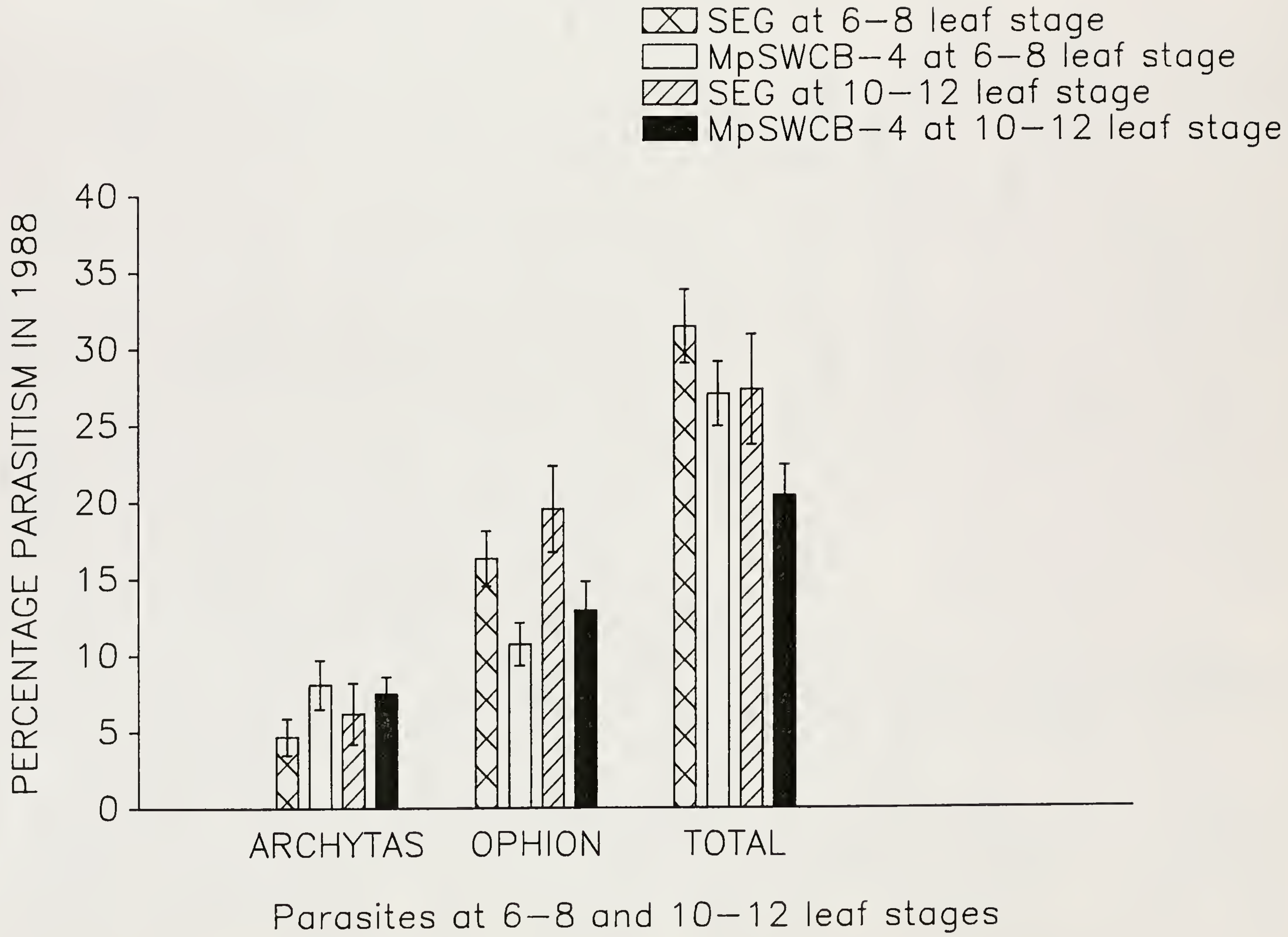

SEG at 6−8 leaf stage
MpSWCB−4 at 6−8 leaf stage
SEG at 10−12 leaf stage
MpSWCB−4 at 10−12 leaf stage
PERCENTAGE PARASITISM IN 1988
0
5
10
15
20
25
30
35
40
ARCHYTAS
OPHION
TOTAL
Parasites at 6−8 and 10−12 leaf stages

Figure 15. Percentages of total parasitization of FAW collected from Stowell's Evergreen (S) and MPSWCB-4 (R) corn in Tifton, Georgia, 1988. *Archytas marmoratus* was artificially applied to both plots.

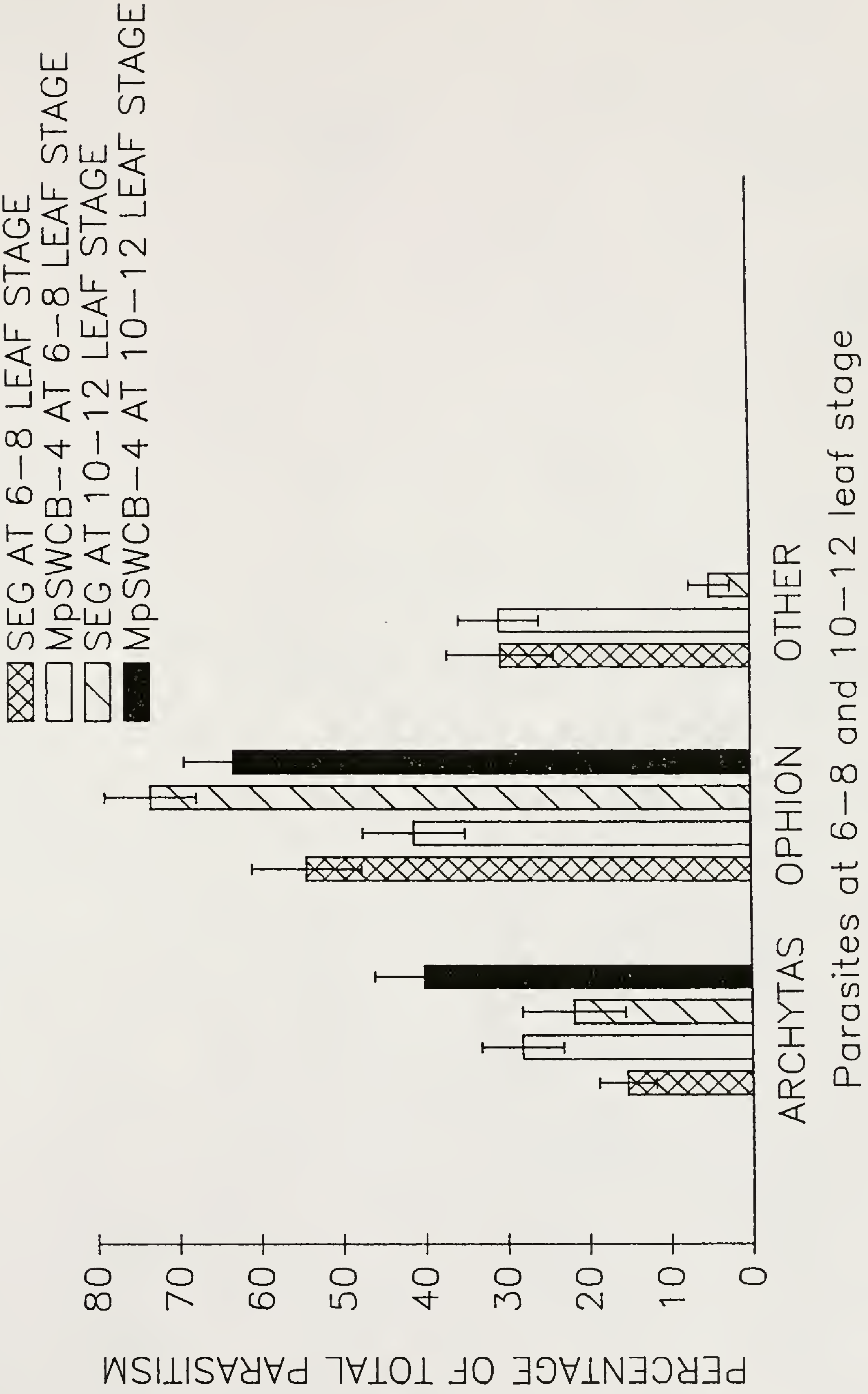

SEG AT 6—8 LEAF STAGE
MpSWCB—4 AT 6—8 LEAF STAGE
SEG AT 10—12 LEAF STAGE
MpSWCB—4 AT 10—12 LEAF STAGE
PERCENTAGE OF TOTAL PARASITISM
0
10
20
30
40
50
60
70
80
ARCHYTAS
OPHION
OTHER
Parasites at 6—8 and 10—12 leaf stage

Figure 16. Percentage parasitization of fall armyworm collected from Stowell's Evergreen (S) and MpSWCB-4 (R) corn plots in Tifton, Georgia, 1989.

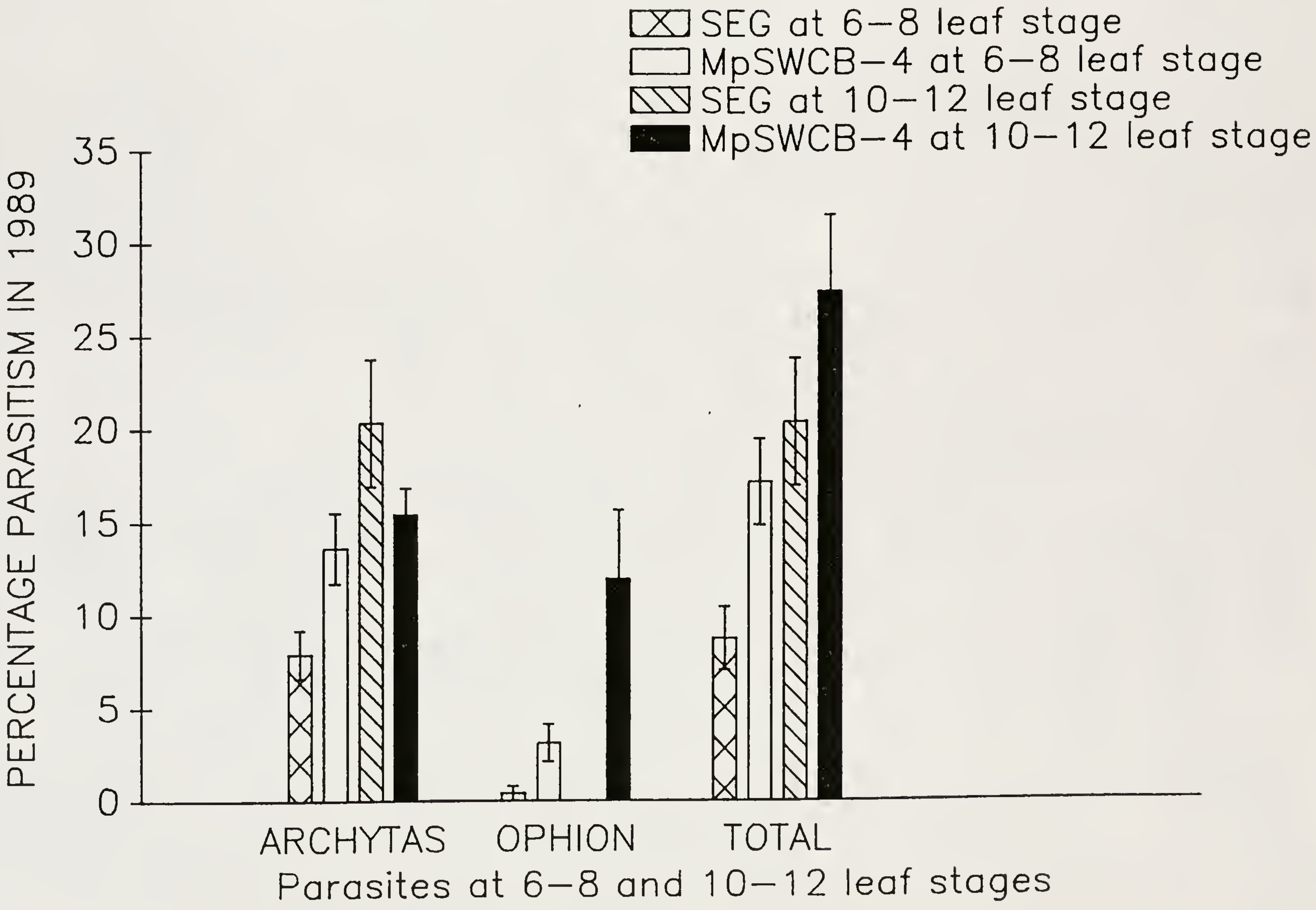
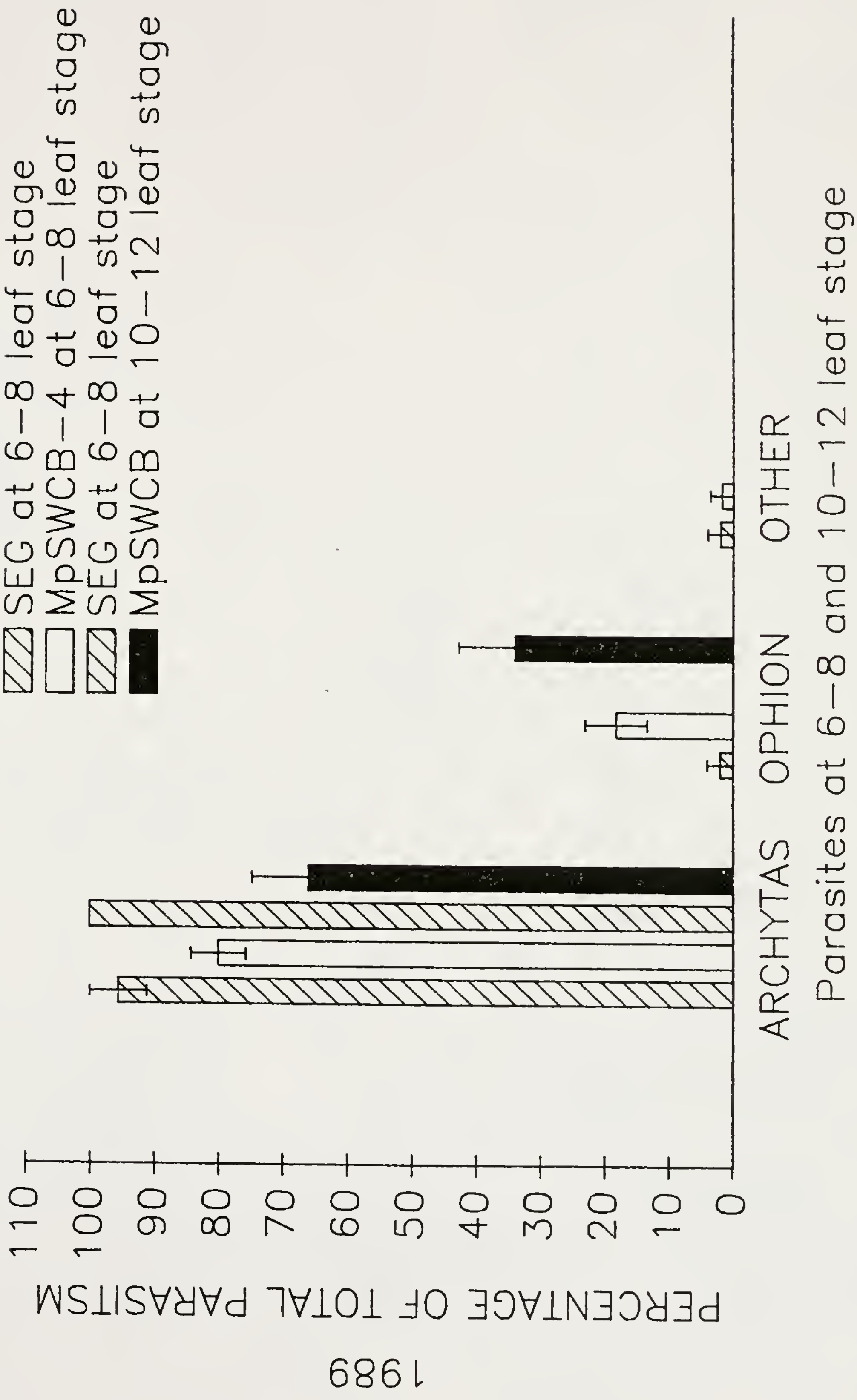

SEG at 6—8 leaf stage
MpSWCB—4 at 6—8 leaf stage
SEG at 10—12 leaf stage
MpSWCB—4 at 10—12 leaf stage
PERCENTAGE PARASITISM IN 1989
35
30
25
20
15
10
5
0
ARCHYTAS
OPHION
TOTAL
Parasites at 6—8 and 10—12 leaf stages

Figure 17. Percentages of total parasitization of fall armyworm larvae collected from Stowell's Evergreen (susceptible) corn and MpSWCB-4 (resistant) corn in Tifton, Georgia, 1989.



SEG at 6—8 leaf stage
MpSWCB—4 at 6—8 leaf stage
SEG at 6—8 leaf stage
MpSWCB at 10—12 leaf stage
ARCHYTAS
OPHION
OTHER
Parasites at 6—8 and 10—12 leaf stage
PERCENTAGE OF TOTAL PARASITSM
0
10
20
30
40
50
60
70
80
90
100
110
1989

highest level of parasitism by Ophion in 1989 was 11%, attained from FAW on MpSWCB-4 at the 10-12 leaf stage.

Compatibility of AM with the resistant corn variety MpSWCB-4 is important. Performance of AM against FAW was not significantly reduced at any time. In 1988 AM performed consistently better on MpSWCB-4 than on SEG (but statistically not significant). There can be a number of explanations for the observed trend of improved performance of AM on MpSWCB-4. AM maggots are not mobile. When applied to the whorl, FAW larvae moving within the whorl due to non-preference factors of resistance permit AM larvae opportunity to parasitize FAW more easily than if the resistance in the plants were not manifested. Thus as the FAW larvae move more within the whorl of the resistant corn, MpSWCB-4, than in the susceptible SEG, there is an increased probability of attack by AM.

Rohlfs and Mack (1985) reported from field studies in Alabama that AM was recovered from all sizes of FAW larvae and the frequency of parasitism of large larvae was not significantly greater than for small larvae during a 2-yr period. They found that rates of adult emergence of the competitor parasitoid O. flavidus generally exceeded those of AM by about 2-fold, but did not differ significantly among the FAW larval developmental stages evaluated. Furthermore, they added that O. flavidus oviposited in FAW larvae of all sizes, but large larvae were most frequently parasitized.

Ophion and other parasitoids prevalent in 1988, were less common in 1989. Rates of parasitism by _Ophion_ were approximately 2-fold higher than _A_. _marmoratus_ in 1988, while this was not the case in 1989. _Archytas_ parasitized 20% of FAW larvae collected from SEG, at the 10-12 leaf stage, while _Ophion_ had its highest level of attack (11%) on FAW on the 10-12 leaf stage of MpSWCB-4. The results of this study indicate that both _A_. _marmoratus_ and _O_. _flavidus_ are capable of impacting populations of fall armyworm in whorl stage corn. This study further indicates that the use of the resistant corn cultivar MpSWCB-4 may enhance their performance. There is the possibility that the use of a resistant cultivar, such as MpSWCB-4, against the FAW which has both non-preference and antibiotic mechanisms of resistance could be antagonistic to enhancement of biocontrol agents that attack later larval instars such as AM or _Ophion_. Results of this study indicate compatibility of the resistant cultivar and AM. Nonpreference factors may stimulate the FAW to move about within the whorl, while antibiosis tends to retard growth and development. A delay in FAW development may not coincide with the most susceptible stage of the larvae for parasitism as compared to FAW developing at a faster rate on SEG. For parasites that attack eggs or small larvae, the use of nonpreference and antibiotic resistance such as that manifested by MpSWCB-4 would be more compatible in combining these two control tactics.

CHAPTER IV

CONSUMPTION, DEVELOPMENT AND FECUNDITY OF FALL ARMYWORM ON STOWELL'S EVERGREEN A SUSCEPTIBLE CORN CULTIVAR AND MpSWCB-4 A RESISTANT CULTIVAR AS AFFECTED BY THE PARASITOID ARCHYTAS MARMORATUS

Slansky (1986) reviewed the impact of insect parasitoids on the physiology and behavior of their hosts within the context of the nutritional ecology of parasitoids and their hosts. An insect host such as the FAW becomes the living space for parasitoids and active defensive responses against parasitoids occur at both behavioral and physiological levels. Nutrient composition of the host hemolymph (e.g., amino acids, proteins and carbohydrates) and fat body (e.g., glycogen) are often altered after parasitization, as are host hormones and metabolic rates (Vinson and Iwantsch 1980).

Slansky (1986) stated "because the genetic fitness of a parasitoid within a host is directly dependent on host activities, natural selection will undoubtedly commonly result in evolution of parasitoid-influenced changes in host physiology and behavior that improve the parasitoids fitness". Also mentioned is the fact that if sufficient nutrients for complete parasitoid development are lacking, then continued feeding by the host will be permitted and perhaps stimulated above the unparasitized level by the

parasite. Soybean looper, *Pseudoplusia includens* (Walker), parasitized by *Copidosoma truncatellum* (Dalman) consumed up to 28% more foliage than unparasitized larvae (Beach and Todd 1986). Conversely, Isenhour (1988), found that two parasitoids of FAW, *Rogas laphygmae* Viereck and *Campoletis sonorensis* (Cameron) were effective in reducing the feeding rate of FAW on corn and sorghum. The present study investigated the FAW larval/pupal parasitoid *Archytas marmoratus* (Townsend) (AM) with respect to the effects of parasitism on host growth and feeding.

Materials and Methods

Insects and Plants

FAW eggs were obtained from a colony maintained at the USDA Insect Attractants and Basic Biology Laboratory, Gainesville, Florida. The colony and experimental conditions were 26.7 ± 1°C, and at least 80% RH. Humidity was maintained in the growth chambers by using a humidifier within the chamber. Larvae were reared on leaves of field grown Stowell's Evergreen corn and MpSWCB-4 corn. Only larvae reared on Stowell's Evergreen corn were used in the parasite study to determine the effect of *A. marmoratus* on feeding by FAW larvae. They were reared in plastic shoeboxes (10 x 30 x 23 cm), 25 larvae per box. Fresh foliage was cut daily and placed in the shoe boxes with five dental wicks saturated with water.

The AM maggots used in this study were mechanically extracted from fecund female AM, obtained from a colony maintained at the USDA Insect Biology and Population Management Research Laboratory in Tifton, Georgia, USA.

Quantitative Performance Studies

Fresh weights of 15 newly molted sixth instar larvae were determined for each cultivar. Fresh leaves fed to the sixth instar larvae were weighed daily to allow measurement of food consumption. Larvae were set up individually in 12 oz clear plastic cups with a standard 10 cm diameter Petri dish serving as a lid. A moistened dental wick was kept in the cup to help maintain high humidity and prevent leaves from drying out. Humidity in the chambers was maintained at 85 % $\pm$ 2 RH. Pre-pupae were removed, dried and weighed. Feces and uneaten leaves were collected and weighed daily to obtain their respective dry weights. A Mettler™ balance H35AR, accurate to 0.1 mg was used for all weighing. All material was dried at 60 $\pm$ 1 ^{0} C for at least 48 hours.

Larval food consumption, growth and food utilization indices were calculated, using gravimetric techniques based on dry weights (Slansky and Scriber 1985). Performance indices included : day 1 pupal dry weight , dry weight gained during the last instar, food utilization efficiencies (AD= Approximate digestibility, ECD = Efficiency of conversion of digested food, and ECI= Efficiency of

conversion of ingested food), relative growth rate,(RGR), and relative consumption rate (RCR). These parameters and their interrelationships are defined in the appendix, A-1 (after Finke 1977).

Fecundity Study

Larvae were reared in plastic shoeboxes as described. Pupae were removed from boxes of each cultivar and sexed, (20 males and 20 females from each cultivar). Separate sexes were placed in plexiglass cages (40x40x40 cm). Upon emergence, males and females from each cultivar were paired in oviposition cages (screen cylinders 20 cm x 9 cm) and provided 'Bounty™' hand towel paper as an oviposition substrate. The paper towel was secured by a rubber band over the top of the cage. Moths were supplied a 10% sucrose solution. All oviposition cages were held in a rearing chamber (Percival incubator model I-35LLs) at 26.2 $\pm$ 1 ^{0} C and 90% RH. Oviposition substrates were removed every second day, and replaced. All surfaces, were checked for eggs and all eggs counted under the microscope.

Experimental Procedure for Parasite Study

To determine the effects of parasitization by AM on foliage consumption and development of FAW, larvae were reared on foliage until the 6th instar on SEG leaves. Mechanically extracted maggots were prepared as described by Gross and Johnson (1985) and suspended in 5 ml of a 0.35% solution of hydroxyethylcellulose (Minidrift, Soilserv Inc.,

Salinas, California).

Newly molted 6th instar larvae were weighed and placed individually in petri-dishes. Sections of whorl tissue approximately 5 x 5 cm each were excised from leaves of field grown SEG and weighed. Using an eye dropper, one drop of maggot solution containing approximately 10 AM maggots was applied to each section of weighed whorl tissue before being placed in a petri dish with the FAW larvae. A dental wick thoroughly saturated with water was also placed in each petri dish to provide moisture and prevent the leaf section from drying up. Larvae were weighed daily and the remaining leaf sections were removed, dried and weighed. Frass was collected daily, dried and weighed until the pre-pupal stage. Pupae were observed for emergence of either FAW adults or AM flies. Data for larvae from which AM flies emerged was tabulated to calculate feeding and growth parameters for parasitized FAW larvae.

It was not possible to distinguish between larvae that had been successfully parasitized by AM and unparasitized larvae in the 6th instar. However, a method was devised to distinguish between parasitized pupae, and unparasitized ones. Normal unparasitized FAW pupae will react to touch by wiggling their posterior end in a spiral or circle. Pupae of parasitized larvae on the other hand do not wiggle at all. Both types of pupae are otherwise similar in appearance.

Larval food consumption, growth and food utilization

indices for AM parasitized and unparasitized 6th instar FAW larvae were calculated as previously described, using gravimetric techniques based on dry weights (Slansky and Scriber 1985). All experimental results were analyzed using a t test (SAS Institute Inc. 1989).

Results and Discussion

Larval dry weights and other developmental parameters of FAW larvae reared on SEG and MpSWCB-4 leaves are summarized on Tables 6 and 7. Larvae reared on MpSWCB-4 leaves had significantly higher body weight (Bi), final weight in the pre-pupal stage (Bf), mean body weight during the sixth instar (MB), amount of food ingested (I), and quantity of frass (F) produced. However, larvae reared on SEG leaves had significantly higher relative growth rate (RGR), efficiency for conversion of digested food (ECD) and efficiency of conversion of ingested food (ECI). Larvae reared on SEG also pupated in significantly less time.

Figure 18 illustrates the fresh weights and dry weights of pupae of FAW reared on SEG and MpSWCB-4 leaves. There was no significant difference in pupal weights. (Sample sizes and data for pupal weights and number of eggs laid by females reared on the 2 cultivars may be found in Table A-7 in the appendix). Figure 19 illustrates the mean number of eggs laid by females reared on SEG and MpSWCB-4 leaves. There was a significant difference in mean number of eggs

TABLE 6. Developmental parameters of fall armyworm 6th instar larvae reared on leaves of a susceptible corn cultivar (Stowell's Evergreen) and a resistant cultivar (MpSWCB-4).

Cultivar	Developmental Parameters[a]						
	Bi	Bf	B	MB	I	F	T
Stowell's Evergreen	11.50 a (0.70)	38.60 a (1.80)	26.80 a (1.80)	22.30 a (0.90)	287.00 a (34.10)	69.90 a (10.00)	4.30 a (0.20)
MpSWCB-4	17.18 b (0.50)	47.60 b (1.70)	30.40 a (1.40)	29.80 b (0.90)	486.60 b (24.30)	122.10 b (5.40)	5.00 b (0.00)

[a] All measurements expressed in mg dry weight; time measured in days. Values expressed as mean (+/- standard error); in each column values not followed by the same letter are significantly different ($p < 0.05$; t test). Parameters are defined in Table A-1. Sample sizes were 9 (Stowell's Evergreen) and 11 (MpSWCB-4).

TABLE 7. Developmental parameters of fall armyworm 6th instar larvae reared on leaves of a susceptible corn cultivar (Stowell's Evergreen) and a resistant cultivar MpSWCB-4.

Cultivar	Developmental Parameters[a]				
	AD	ECD	ECI	RCR	RGR
Stowell's Evergreen	0.74 a (0.03)	0.15 a (0.02)	0.01 a (0.01)	2.97 a (0.31)	0.28 a (0.01)
MpSWCB-4	0.74 a (0.01)	0.09 a (0.00)	0.06 b (0.00)	3.22 a (0.15)	0.20 b (0.01)

[a] Parameters defined in Table A-1. Values expressed as mean (+/- std. error); in columns, values not followed by the same letter are significantly different ($p < 0.05$; t test). Parameters are defined in Table A-1. Sample sizes were 9 (Stowell's Evergreen) and 11 (MpSWCB-4).

Figure 18. Fresh weight and dry weight of pupae of fall armyworm reared on leaves of Stowell's Evergreen corn (susceptible cultivar) and MpSXCB-4 corn (resistant cultivar)

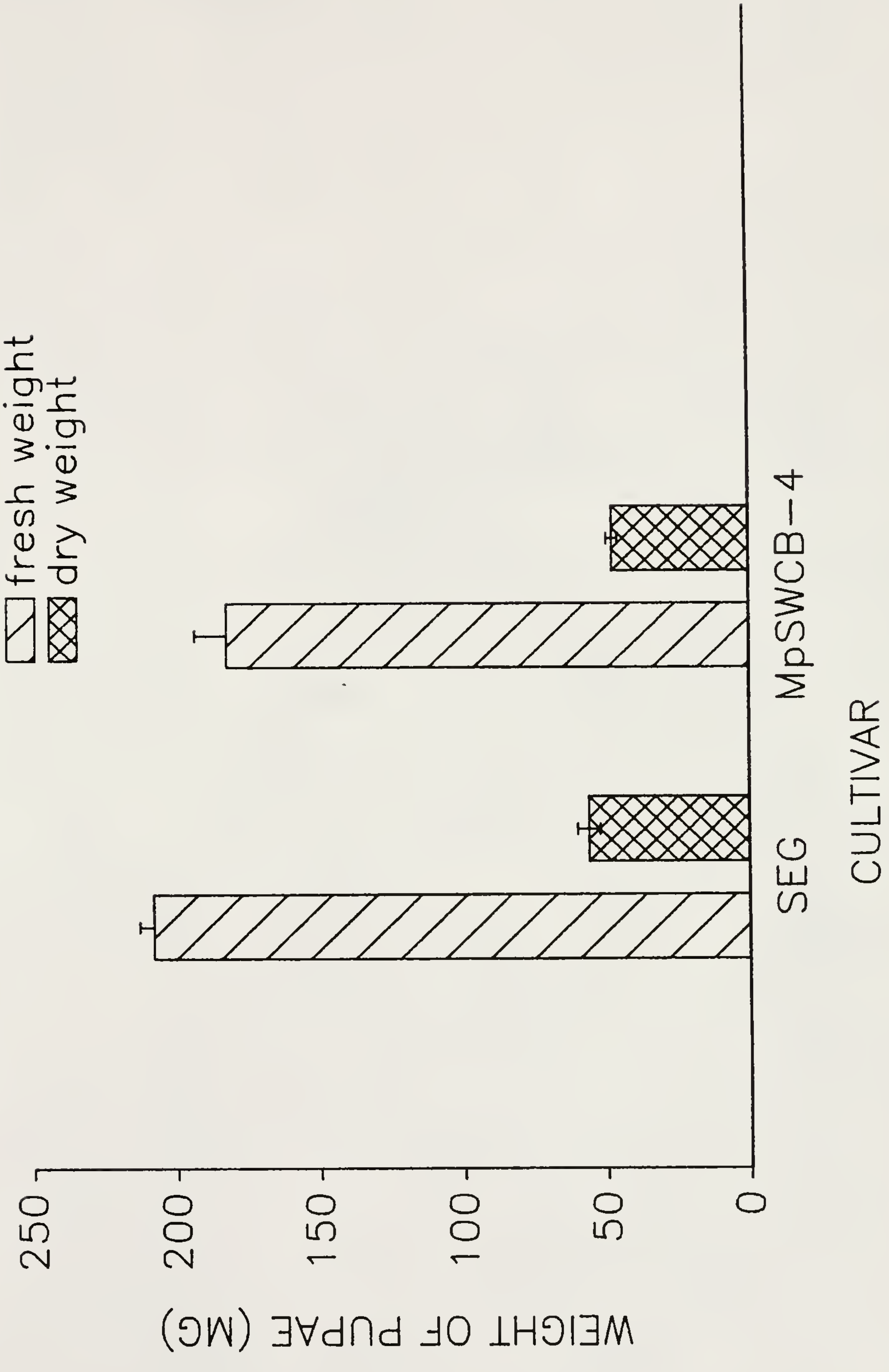
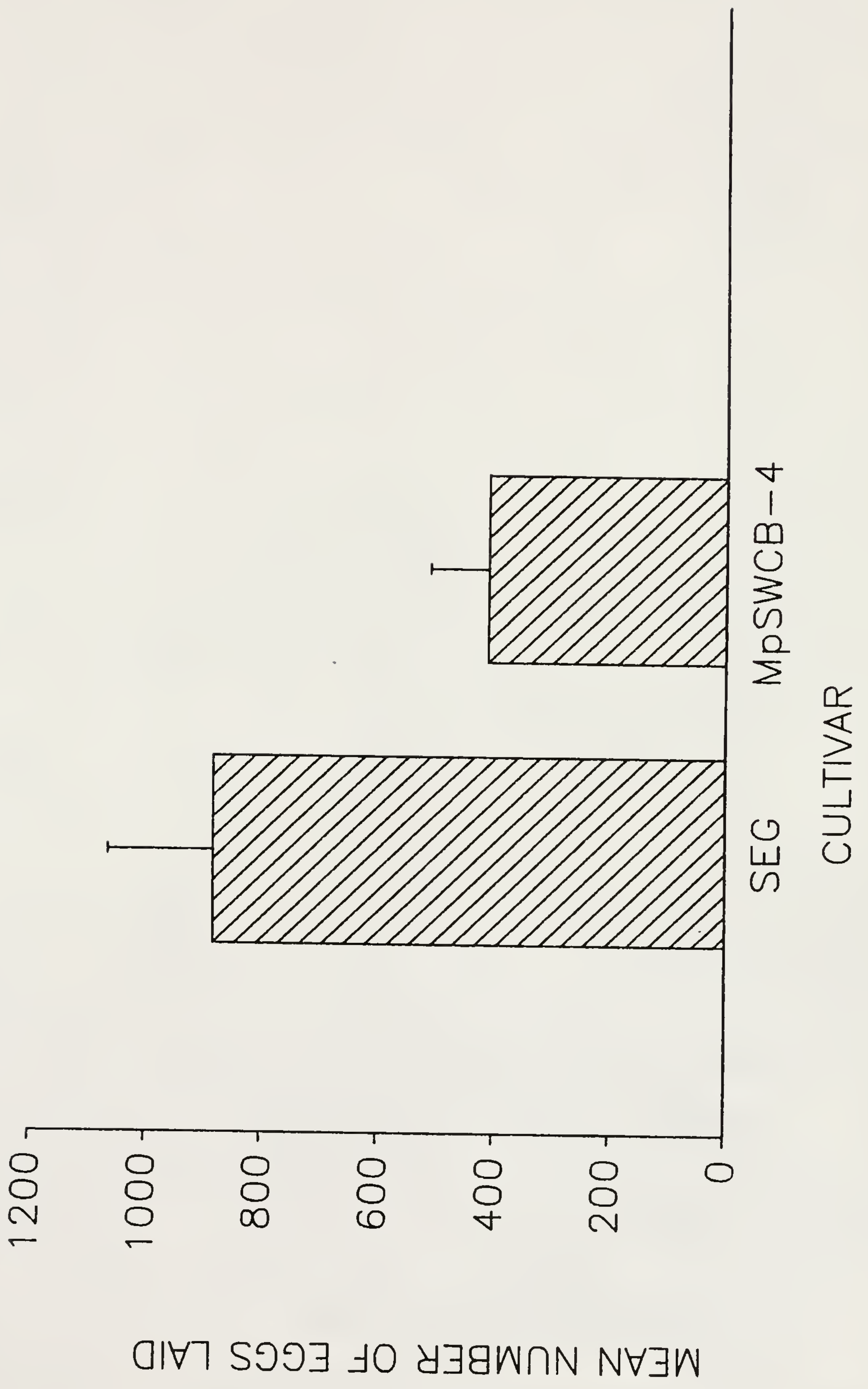

WEIGHT OF PUPAE (MG)
250
200
150
100
50
0
fresh weight
dry weight
SEG
MpSWCB-4
CULTIVAR

Figure 19. Mean number of eggs laid by fall armyworm females reared on leaves of Stowell's Evergreen corn (susceptible cultivar) and MpSWCB-4 corn (resistant cultivar).



MEAN NUMBER OF EGGS LAID
0
200
400
600
800
1000
1200
SEG
MpSWCB—4
CULTIVAR

Figure 20. Fresh weights of 6th instar fall armywrom larvae parasitized by _Archytas marmoratus_, and unparasitized larvae.

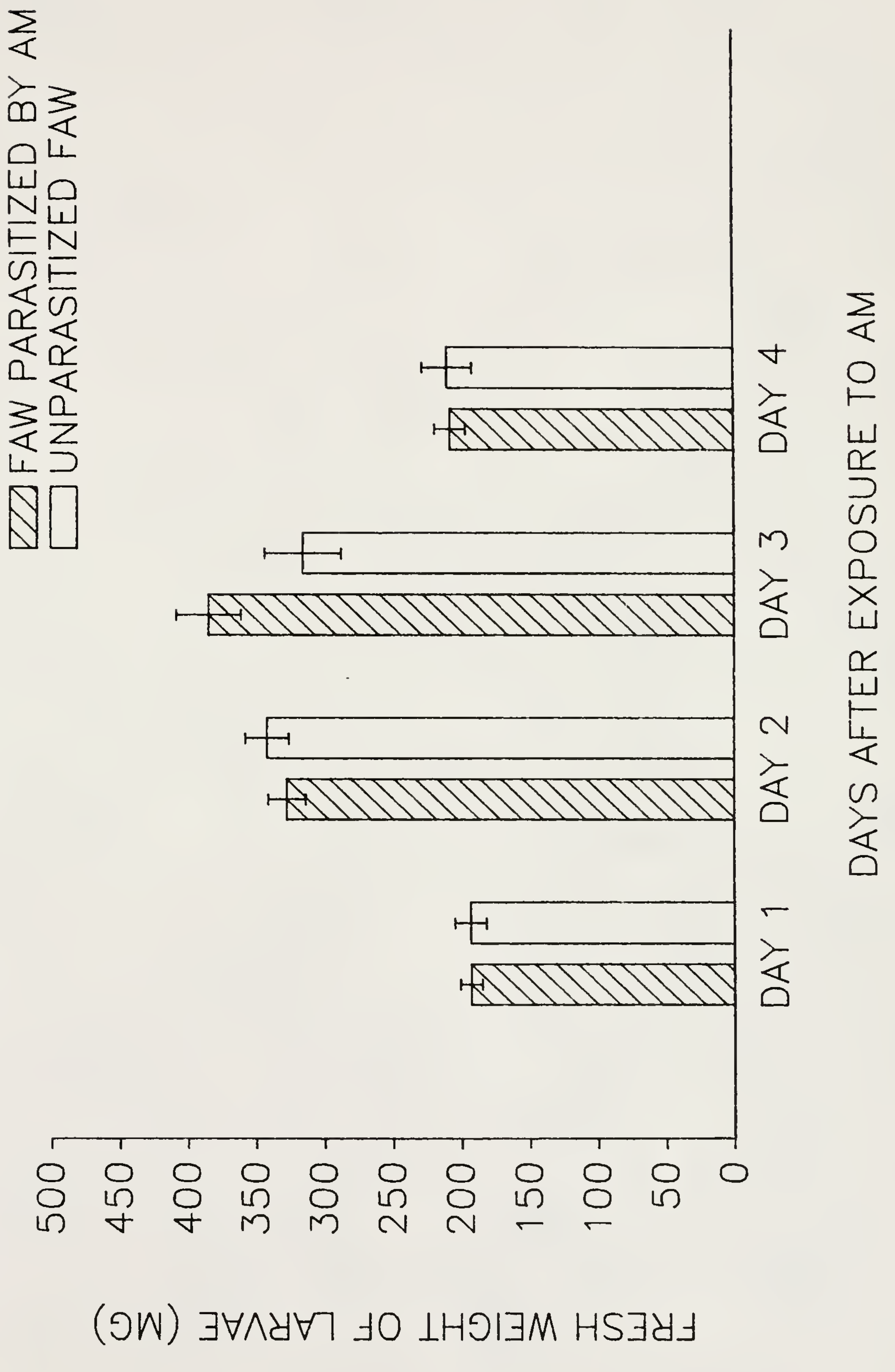

FAW PARASITIZED BY AM
UNPARASITIZED FAW
FRESH WEIGHT OF LARVAE (MG)
0
50
100
150
200
250
300
350
400
450
500
DAY 1
DAY 2
DAY 3
DAY 4
DAYS AFTER EXPOSURE TO AM

TABLE 8. Effect of parasitism by _A_. _marmoratus_ on FAW larvae. Consumption, growth and biomass parameters.

	Developmental Parameters[a]					
	Bi	Bf	MB	B	I	F
Parasitized larvae	18.39 a (1.21)	43.84 a (1.45)	18.39 a (1.21)	33.76 a (1.09)	140.30 a (9.70)	69.54 a (5.37)
Unparasitized larvae	19.53 a (1.52)	45.02 a (2.10)	19.53 a (1.52)	34.29 a (1.65)	125.67 a (8.76)	64.81 a (6.77)

All parameters defined in Table A-1. Values expressed as mean (+/- std error); in columns, values not followed by the same letter are significantly different ($p < 0.05$; t test).

TABLE 9. Effect of parasitism by _A. marmoratus_ on last instar fall armyworm feeding efficiencies, consumption and growth rates.

	Developmental Parameters[a]				
	AD	ECD	ECI	RCR	RGR
Parasitized larvae	0.49 a (0.03)	0.31 a (0.03)	0.14 a (0.01)	4.1 a (0.24)	0.55 a (0.03)
Unparasitized larvae	0.49 a (0.03)	0.32 a (0.02)	0.16 a (0.01)	3.6 b (0.14)	0.57 a (0.04)

[a] All parameters defined in Table A-1. Values expressed as mean (+/- std error); in columns, values not followed by the same letter are significantly different ($p < 0.05$; t test).

laid, with females reared on SEG leaves laying significantly more eggs than females reared on MpSWCB-4 leaves.

Fig. 20 illustrates the mean fresh weights (mg) of parasitized and unparasitized 6th instar FAW larvae for 4 days after introducing the parasite. There was a slight increase in body weight of 3 day old parasitized larvae over unparasitized larvae. Analyses over days did not indicate any significant difference in weights between the parasitized and unparasitized larvae, however.

Larval dry weights and other developmental parameters are presented in Table 8. Parasitized FAW had a significantly higher RCR than did unparasitized FAW larvae (Table 9). There were no significant differences among any of the other developmental parameters.

Food intake, utilization and allocation can be altered in an adaptive manner in response to extrinsic and intrinsic factors (Slansky and Rodriguez, 1987). Increase in foliage consumption displayed by parasitized larvae is well known (e.g., Beach and Todd (1986) and Hunter and Stoner (1975). This may represent an adaptation in response to the parasite. A parasitized larva is supporting not only itself but also the parasitoid, and may adapt to the situation by increasing its own total ingestion.

Slansky and Scriber (1985) stated that effects of parasitoids include substantial impact on the consumption and utilization of food by their hosts, whereas host developmental time seems to be less frequently affected.

Slansky (1986) discussed two possible effects the parasitoid can have on a host, with some hosts exhibiting an increase in feeding and others causing an inhibitory effect which results in the host decreasing its food consumption. Thompson (1982) pointed out that, in general, species of ichneumonid parasites reduce growth rates of their hosts to a greater extent than braconid species, and growth rates are reduced more severely in the last instars. The implications of increased consumption by parasitized larvae needs to be addressed in considering the employment of Archytas marmoratus in IPM.

CHAPTER V

EFFECT OF RESISTANT AND SUSCEPTIBLE CORN CULTIVARS ON MICROSOMAL MONOOXYGENASES AND INSECTICIDE SUSCEPTIBILITY OF THE FALL ARMYWORM

General Description of Mixed Function Oxidases

Mixed function oxidases (MFO), also referred to as cytochrome P-450-dependent monooxygenases, are the most important detoxification enzymes in insects and are associated with the endoplasmic reticulum, a cell membrane. The term "mixed function" oxidases refers to the fact that their action reduces oxygen, produces H_2O, and there is concomitant oxidation of the substrate (Hodgson 1983a). The second name, monooxygenases, relates to oxidation reactions that always result in the insertion of one oxygen atom into the xenobiotic molecule. In insects, the main tissue sources of these enzymes are the fat body and the midgut (Krieger *et al*. 1976; Wilkinson and Brattsten 1972).

The MFO system is characterized by (1) requiring NADPH as a co-factor for activity, (2) requiring molecular oxygen, and (3) having a broad substrate specificity. The MFO system is capable of oxidizing many xenobiotics and endogenous compounds.

1. Electron transport system

The microsomal oxidase system is actually a system of 2 enzymes and a co-factor as shown in figure 21. The enzymes appear to be embedded in the endoplasmic reticulum in such a way that more polar or water soluble compounds do not make contact whereas less polar, lipid soluble compounds are contacted, providing selectivity for lipophilic xenobiotics. The insect MFO system has been thoroughly reviewed by Wilkinson and Brattsten (1972) and Hodgson (1983).

Oxidation is accomplished by a flow of electrons from NADPH (generated elsewhere in the cell) to the flavoprotein (FP), NADPH-cytochrome P-450 reductase (CPR), and then to an enzyme known as cytochrome P-450. Phosphatidylcholine is also necessary for activity. Cytochrome P-450 binds both the xenobiotics and oxygen and then splits the oxygen to introduce an atom into the substrate. The oxidized xenobiotic is then ejected and cytochrome P-450 goes on to oxidize another molecule. Within the microsomal particles, NADPH requiring oxidation activity generally concentrates in microsomes containing smooth endoplasmic reticulum.

Cytochrome P-450 is the most important component of a number of monooxygenase systems. It is known to occur in many groups of animals, plants and microorganisms and was first described in insects by Ray (1967). The role of cytochrome P-450 in the metabolism of insecticides is discussed in Hodgson (1978).

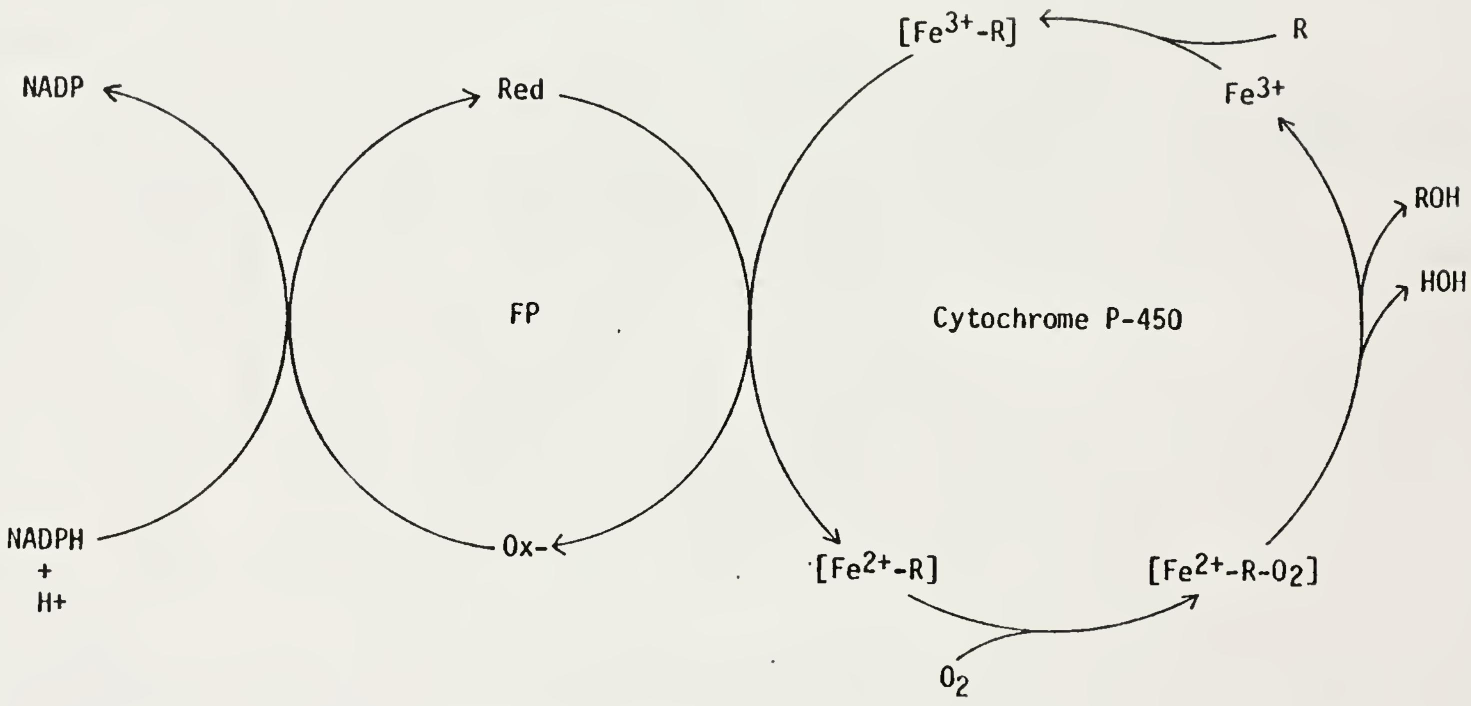


Fig. 21 Schematic representation of the cytochrome P-450-dependent microsomal MFO system.

2. Substrate Specificity

Detoxification of xenobiotics can be divided into primary and secondary reactions. The primary reactions involve oxidation, hydrolysis, reduction, and glutathione conjugation of xenobiotics to produce polar end-products, while the secondary reactions result in water soluble conjugates. There are 3 main enzyme systems that are dominant in primary reactions. These are (1) microsomal oxidases, (2) hydrolases and (3) glutathione S-transferases.

Oxidation reactions involving microsomal oxidases are by far the most important. This is because nearly all of the functional groups found in lipophilic organic compounds are susceptible to microsomal oxidation or are attacked by the system. The most important of these are

1. Epoxidation, $R - CH = CH - R^1 \longrightarrow R - \overbrace{CH - CH}^{O} - R^1$
2. Sulfoxidation, $R - S - R^1 \longrightarrow R - \overset{O}{\overset{\|}{S}} - R^1$
3. Desulfuration, $R_1\ R_2\ \overset{S}{\overset{\|}{P}} - X \longrightarrow R_1\ R_2\ \overset{O}{\overset{\|}{P}} - X + S$
4. N, or O dealkylation, $R - (NH, O) - CH_3 \longrightarrow R - (NH_2, OH) + CH_2O$
5. Hydroxylation, $R - CH_3 \longrightarrow R - CH_2OH$

Not all of reactions result in detoxification. The sulfoxidations and phosphorothioate oxidations

(desulfurations) nearly always result in "activation" of the toxic molecule, increasing its toxicity. Some of the products containing the oxygen analogs P = 0 or S = 0 bind more tightly to the enzyme acetyl cholinesterase (ACLE) resulting in stronger inhibition (Corbett, 1975). Epoxidation also can result in activation. Aldrin is converted to dieldrin and heptachlor to its epoxide. Epoxides are more stable than their precursors and therefore their persistence is increased. Some epoxides also are carcinogenic and are environmental pollutants. They are reactive and may form covalent bonds with DNA (Corbett, 1975).

The MFO also are important because one of the functional groups attacked by the system is present in nearly every pesticide. Almost any biologically active compound can be degraded by the enzymes. Development of resistance seems to be associated with a general increase in all types of MFO activity (Cassida, 1969).

MFO play an important part in feeding since all plants contain defensive compounds, some of which are toxic. Terriere (1984) discussed that some host plants of phytophagous insects induce MFO, and speculated that the phenomenon of induction may have evolved from the interactions between herbivorous insects, their host plants and an adaptation in feeding.

The effects of host plants and allelochemicals on MFO, and insecticide susceptibility have been researched in several phytophagous insects, including the fall armyworm (Yu, 1982a).

The concept of induction of MFO may prove to be important in pest management, especially since there is evidence of induction by host plants. Yu (1982) found corn fed fall armyworm to be more tolerant of certain insecticides than soybean fed fall armyworm. An insect pest may require different amounts of insecticides for control on different plants.

Yu (1985) further demonstrated how host plants that can induce detoxication enzymes in herbivorous insects and that this may result in decreasing insecticide toxicity, while these same enzymes can activate proinsecticides to active insecticides in some cases. Microsomal desulfuration and sulfoxidation of phosphorothionate and thioether-containing insecticides, respectively, are typical examples of such oxidative activation. If a host plant can stimulate these organophosphate (OP) activation enzymes in insects, such induction would increase an insects susceptibility to insecticides that are activated by the MFO. It may be possible to control such an insect by applying lower rates of appropriate insecticides to crops which possess inducing capability.

In the present study, the effects of feeding on the susceptible corn cultivar, Stowell's evergreen, the resistant corn cultivar, MpSWCB-4, and diet containing silks of the resistant corn _Zapalote Chico_ on the MFO of FAW sixth instar, were determined. Further, the susceptibilities of the fall armyworm reared on the susceptible corn cultivar Stowell's

Evergreen and the resistant cultivar MpSWCB-4 were determined for three commonly used pesticides. The three compounds representing three different groups of insecticides were methomyl, a carbamate, dursban, an organophosphate, and bifenthrin, a synthetic pyrethrin.

Materials and methods

Plants and Diets.

Seeds of 2 corn genotypes "Stowell's Evergreen" (SEG), a sweet corn and "MpSWCB-4" (-4) were obtained from Dr. B. R. Wiseman of the USDA in Tifton, Georgia, and planted in Gainesville, Florida. Standard cultural practices were employed with respect to fertility and weed control. No soil or foliar insecticides were used. SEG is a susceptible corn, while MpSWCB-4 is a cultivar that was developed for leaf-feeding resistance to the southwestern corn borer, *Diatraea grandiosella* (Dyar); however, it also has leaf-feeding resistance to the FAW (Davis et al. 1978). Plants were grown in large black plastic pots (25 cm x 25 cm) in the greenhouse, in the field behind the USDA Attractants Laboratory in Gainesville, and in an environmental chamber with an extended photoperiod (14-hour). Painter (1951) indicates that the resistant plant is always resistant under the same environmental conditions. If the environment changes, the level of resistance may change, but not always.

A third cultivar of corn used in the experiments was "Zapalote Chico" (ZC). Wiseman and Widstrom (1986) reported

evidence that both non-preference and antibiosis resistance to feeding are manifested in the silks of ZC to FAW and Helicoverpa zea (Boddie). ZC (Zapalote Chico) is a dent corn. Leaves of SEG and MpSWCB-4 were fed to FAW larvae while silks of "Zapalote Chico" were incorporated into a pinto bean meridic diet for FAW, as described earlier.

Fresh silks of ZC were excised and blended in 100 ml distilled water and mixed with 300 ml of a pinto bean meridic diet for FAW. A silk concentration of 5, 10, and 20 g per 300 ml of diet was used to represent a gradient of resistant diets. The diet/plant silk mixture was dispensed into 1 oz plastic cups and allowed to solidify for 2 hrs.

Insects.

Larvae were reared on leaves of SEG, MpSWCB-4, or on a Zapalote Chico silk/artificial diet. Eggs were obtained from the USDA laboratory in Gainesville, Florida. The larvae were maintained in covered plastic boxes (10 x 22 x 31 cm.), 20 per box, in environmental chambers at 25°C with a 16:8, L:D photoperiod. Humidity within the chambers was maintained at 80% ± 5. Only sixth instar larvae were used for both enzyme assays and bioassays for insecticide susceptibility. Newly molted fifth and sixth instars were always synchronized to be of the same physiological age for experiments.

Chemicals

Analytical grade aldrin and dieldrin were obtained from

Shell Chemical Company, Modesto, California, as was methomyl (Nudrin[R]) (99% purity). Chlorpyrifos (Dursban[R]) (97.7% purity) was obtained from Dow Chemical Company, Midland, Michigan. Bifenthrin (Capture[R]) (94.4% purity) was supplied by FMC Corporation, New York. All reagents used were of the highest purity commercially available.

Newly molted sixth instar larvae (less than 3 hr after ecdysis) which had been maintained on various experimental diets (i.e., CK, SEG, ZC-5 g, ZC-10 g, ZC-20 g, SEG leaves or MpSWCB-4 leaves) were randomly divided into groups of 5 larvae. In some experiments, larvae were reared until sixth instar, and then fed for 2 days prior to being used for enzyme assay or insecticide bioassay. In most cases however they were reared from eggs through the sixth instar on leaves excised from SEG or MpSWCB-4 corn plants.

Enzyme Preparation

Groups of 5 midguts were dissected from 2 day old sixth instar FAW larvae reared on the appropriate diet. All gut contents were removed. This was done by excising the anterior portion of the body just behind the metathoracic legs and the posterior portion of the body just behind the fourth pair of prolegs. The entire larval gut was removed anteriorly and placed on a paper tissue, and the gut contents effectively removed using fine forceps. The tissue was immediately washed in ice-cold 1.15% KCl and homogenized in 20 ml ice-cold 0.1 M sodium phosphate buffer, pH 7.5, in a motor driven tissue

grinder for 30 sec. The homogenate was filtered through cheesecloth and immediately used as the enzyme source. The protein concentration of each preparation was determined by the method of Bradford (1976), using bovine serum albumin as the standard.

Enzyme Assays

The activity of aldrin epoxidase was measured as a representative microsomal oxidase. MFO activity of FAW has been investigated by Yu (1982). The incubation mixture for determination of epoxidase activity had a total volume of 5 ml and contained 2 ml of tissue homogenate; 0.1 M sodium phosphate buffer, pH 7.5; an NADPH generating system consisting of 1.8 umol of NADPH, 18 umol of glucose-6-phosphate, and one unit of glucose-6-phosphate dehydrogenase and 250 nmol of aldrin as the substrate.

All incubations were carried out in a water bath with shaking at 30 $\pm$ 2oC in an atmosphere of air for 15 min. Epoxidase reactions were stopped with 10 ml of hexane. All incubations were done in duplicate. Extraction was performed by slow shaking at about 60 oscillations per minute in a shaker, for 1 hour. The water and hexane layers were then separated by centrifugation. The water layer was removed with a syringe, and the hexane layer was dried over anhydrous sodium sulphate. The product, dieldrin, was analyzed using a gas liquid chromatograph, Varian Model 3740, equipped with an electron capture detector. A 4 ft. x 2 mm i.d. glass column

packed with a 1:1 mixture of 5% DC-11 and 5% QF-1 on 100-200-mesh high-performance Chromosorb W was used. The operating conditions were 185°C; detector 250°C; injector port, 200°C; and nitrogen carrier gas, 30 ml/min. Quantities of dieldrin were determined by measuring the peak height. Standards of dieldrin were run between samples.

Bioassays.

Stock solutions of the carbamate methomyl, the organophosphate chlorpyrifos, and the synthetic pyrethroid bifenthrin were prepared using acetone as the solvent. A series of dilutions were prepared for each compound. Larvae were weighed in groups of 5 to determine mean larval weight. Two-day-old final instar larvae were collected from their various diet groups and treated on the thorax dorsum with each insecticide in 1 ul acetone using a hand held topical applicator. Controls were treated with 1 ul of acetone only. After treatment, the insects were kept in 1 oz plastic cups containing about 2 g of diet on which they were reared. Tests with each insecticide were replicated three times with 100 insects per replicate, 20 insects per concentration. Mortality counts were made after 24 and 48 hrs. Several preliminary experiments were carried out to establish the appropriate dosage range for each treatment. Each insecticide was tested at a minimum of five concentrations. Probit analyses were performed on bioassay data by the method of Finney (1971). LD_{50}'s were considered significantly different

if the 95% fiducial limits did not overlap.

Results and discussion

Table 10 shows that the MFO levels of FAW reared on leaves of resistant corn cultivar MpSWCB-4 were only slightly higher than those of FAW reared on the leaves of the susceptible corn cultivar SEG. Aldrin epoxidase activity was significantly higher for larvae fed field grown MpSWCB-4 leaves than for larvae fed field grown SEG leaves, growth chamber grown MpSWCB-4 leaves, and greenhouse grown MpSWCB-4 leaves.

The inhibition of aldrin epoxidase was observed when silks of Zapalote Chico corn were mixed into artificial diet in increasing quantities (Table 11). There was a significant decrease in epoxidase activity for larvae fed ZC 10 g and ZC 20 g diets. There was no significant difference in aldrin epoxidase activity for larvae fed the ZC 5 g when compared to the control diet.

The FAW may not be stressed by the induction of MFO noted with MpSWCB-4; however the presence of some component of Zapalote Chico silks which appears to inhibit MFO, may relate to the poor performance of FAW on diets containing ZC

TABLE 10. Aldrin epoxidase activities of Fall armyworm Larvae fed various diets of resistant and susceptible corn cultivar leaves.

Diet		Aldrin epoxidase pmol/min/mg protein[b]	Larval body weight (g F.W.)
Meridic diet		147.21 ± 9.23 c	0.33 ± 0.02
Stowell's Evergreen	(R)[a]	156.58 ± 5.52 c	0.30 ± 0.001
MpSWCB-4	(R)	189.47 ± 9.24 b	0.29 ± 0.01
Stowell's Evergreen	(F)	189.72 ± 3.82 b	0.29 ± .001
MpSWCB-4	(F)	231.14 ± 3.24 a	0.30 ± .01
Stowell's Evergreen	(C)	128.63 ± 1.17 d	0.36 ± 0.02
MpSWCB-4	(C)	192.26 ± 4.48 b	0.28 ± 0.01
Stowell's Evergreen	(GH)	189.68 ± 10.58 b	0.29 ± 0.03
MpSWCB-4	(GH)	200.36 ± 10.51 b	0.28 ± 0.01

[a] (R) = Two day old sixth instar larvae reared from eggs on leaves
(F) = Larvae reared till newly molted sixth instar on meridic diet, then on field grown leaves for 2 days prior to assay
(C) = Larvae reared till newly molted sixth instar on meridic diet, then on laboratory growth chamber grown corn leaves for 2 days prior to assay.
(GH) = Larvae reared till sixth instar on meridic diet, then on greenhouse grown corn leaves for 2 days prior to assay.

[b] Mean ± SE of at least 2 experiments, each in duplicate

In columns, values not followed by the same letter are significantly different ($p < 0.05$ Scheffe's).

TABLE 11. Microsomal oxidase activities of fall armyworm larvae fed a meridic diet containing various concentrations of silks of a resistant corn cultivar (Zapalote Chico) and a susceptible corn cultivar (Stowell's Evergreen).

Diet[a]	Aldrin epoxidase[b] (pmol/min/mg protein)	Larval weight at assay (gm F.Wt.)
Meridic diet	147.21 ± 9.23	0.33 ± 0.02
Zapalote chico 5 g	133.06 ± 1.25	0.31 ± 0.002
Zapalote chico 10 g	110.45 ± 3.53	0.33 ± 0.01
Zapalote chico 20 g	94.29 ± 1.91	0.31 ± 0.01

[a] Newly molted sixth-instar larvae were fed diet containing silks for 2 days prior to enzyme assays.
[b] Mean ± SE of three experiments, each with duplicate determinations.

silks because the same constituents may be detrimental to larval survival and growth.

The induction of microsomal oxidases by host plants in the fall armyworm has been documented (Yu 1982). This inductive effect may result in a higher pesticide treatment rate for one crop than for another to obtain the same degree of control. Yu (1986) stated that an important aspect of research in plant-insect interactions is to learn whether insecticide activation enzymes can be stimulated and to explore consequent effects on the toxicity of insecticides to insects. Results reported here, in conjunction with those reported elsewhere on induction of MFO and effects on insecticide susceptibility can be used to improve insecticide efficacy against fall armyworm, and possibly lead to a reduction in pesticide usage.

The relative potency of the three insecticide classes in the topical assays toward FAW was pyrethroid > carbamate > organophosphate. FAW reared on the susceptible cultivar SEG was more susceptible to both methomyl and bifenthrin, with LD_{50}'s of 2.39 ug/g larva and 0.45 ug/g larva, respectively, than FAW reared on the resistant corn cultivar MpSWCB-4 with LD_{50}'s of 4.19 ug/g larva and 1.29 ug/g larva, respectively. Bifenthrin was the most toxic among the 3 insecticides tested. Table 12.

The organophosphate chlorpyrifos was, however, more toxic to larvae reared on the resistant corn MpSWCB-4 than to larvae reared on the susceptible SEG. Since the 95%

TABLE 12. Toxicity of insecticides applied topically to the Fall armyworm reared* on a susceptible and resistant corn cultivars.

	FAW on SEG		FAW on MPSWCB-4	
Insecticide	Slope ± SE	LD_{50} (95% FL)	Slope ± SE	LD_{50} (95% FL)
Methomyl	2.975 ± 0.16	2.39 (1.84- 3.17)	2.909 ± 0.20	4.19 (3.23- 5.54)
Chlorpyrifos	2.616 ± 0.24	16.43 (11.80-21.72)	2.234 ± 0.23	8.85 (3.53-12.35)
Bifenthrin	2.893 ± 0.30	0.45 (0 .34- 0.61)	3.877 ± 0.25	1.29 (1.04- 1.64)

* All plants were field grown, and fresh leaves fed to insects from egg stage till 2 day old sixth instar.

fiducial limits overlap slightly, the toxicities were not considered to be significantly different. This reversal in relative toxicities may be due to numerous factors, one being the structure of the insecticide and the way in which it potentially can be metabolized. Mixed function oxidase experiments indicated that FAW reared on resistant MpSWCB-4 leaves had slightly higher aldrin epoxidase activity than those reared on susceptible corn. The metabolism of organophosphate insecticides by microsomal oxidases often constitutes an activation reaction where the resulting compound of sulfoxidation or desulfuration is actually more toxic than its precursor. An increase in MFO results in an increase in toxicity and susceptibility to an insecticide metabolized through an activation reaction. It is reasonable to speculate that the increased MFO activity observed in FAW reared on resistant corn may be attributable to an increase in susceptibility to the organophosphate insecticide chlorpyrifos. Yu (1986) discusses that elevated desulfurase activity may result in certain organophosphates (with the P = S moiety) being more toxic to the fall armyworm.

The carbamate methomyl and the pyrethroid bifenthrin are not metabolized by activation reactions. There are numerous other detoxification enzymes that may have been induced or inhibited by allelochemicals in the corn cultivars used. These may have been responsible for the

significant decrease in toxicity towards larvae reared on

resistant corn leaves.

Yu (1988) showed that pyrethroids possess selective toxicity in favor of entomophagous insects but are highly toxic to lepidopterous insect pests. He concludes that pyrethroid insecticides should be ideal for controlling lepidopterous pests and sparing their natural enemies such as spined soldier bugs. The data shown here indicate that less insecticide may be necessary for control of FAW on susceptible corn and more on resistant corn, if the insecticide is a pyrethroid or a carbamate. The reverse applies if the compound is an organophosphate. The fact that more insecticides may be required on some resistant corn emphasizes the need for research on compatibility of pest management tactics in an IPM program.

CHAPTER VI

SUMMARY AND CONCLUSIONS

The effects of feeding on Zapalote Chico, a resistant cultivar of corn [*Zea mays* (L.)] by *Spodoptera frugiperda* (J. E. Smith), (FAW), was investigated. Also investigated was the effect of the parasitoid *Archytas marmoratus* (Townsend) on FAW feeding and growth. The tri-trophic interactions among a resistant variety of corn (MpSWCB-4), FAW, and *A. marmoratus*, a natural enemy of FAW, was evaluated. Field experiments were conducted over two years to determine the compatibility of MpSWCB-4, a resistant cultivar of corn, and the FAW natural enemy *A. marmoratas*. Effects of feeding on MpSWCB-4 and Zapalote Chico corn on the detoxification enzymes of FAW, as well as on susceptibility to 3 groups of insecticides, were determined.

Results of these experiments make possible the suggestion of possible strategies that can be applied toward the integrated pest management of FAW on corn. Where parasitoids that attack late instars of insect pests are evaluated for their impact on a pest, plant damage by the pest occurs for most of the life cycle of the pest. Plant resistance may be employed to lessen the damage and/or reduce the populations in the next generation of the pest.

This project supports the idea that the mechanisms of plant resistance must be understood to implement them correctly within the context of an Integrated Pest Management system in corn. If a resistant cultivar is only "tolerant", meaning it can withstand damage, the pest will be physiologically unaffected by the resistant cultivar. Any predators and parasites of a pest in such a situation will not be affected adversely by the resistant cultivar. Nonpreference may cause behavioral abnormalities such as stimulating larvae to move about more. This may result in the pest increasing its exposure to predators and parasitoids. Antibiosis can cause death, but more often causes retardation of growth and development, possibly permitting parasitoids and predators that attack small larvae to effect greater parasitism.

Wheeler and Slansky (in press) discussed compensatory responses of FAW when fed water and cellulose-diluted diets. They demonstrated the compensatory feeding ability of FAW in response to diets diluted with cellulose or water. The feeding study determined some effects of feeding on silks of the resistant cultivar Zapalote Chico of FAW also demonstrated the compensatory ability of FAW to adapt to diets containing antibiotic factors.

The feeding inhibition/toxicity study showed that certain quantities of ZC silk in the meridic diet proved to be toxic to FAW (e.g., 10 g and 20 g in 300 ml of meridic

diet). This toxicity may be the direct cause of a reduction in relative growth and relative consumption rates. Decreased efficiency to convert ingested food into insect tissue and the significant decrease in mean body weight also appears to have been a result of a toxic factor in the ZC silks. Toxicity may have been the underlying cause of the observed increase in developmental time, decreased pupal weights and decreased fecundity for FAW feeding on the silk diets. Feeny (1975) suggested that certain compounds (allelochemicals) in plants act as qualitative barriers to herbivorous insects. These may be effective in small amounts against herbivores not adapted to feeding on such compounds but are vulnerable to the evolution of counter adaptations. In these circumstances, such compounds may have little or no dosage-dependent effects on the growth of insects adapted or specialized at feeding on plants containing them.

The mixed function oxidases of FAW were affected adversely by feeding on ZC silks, since enzyme inhibition was detected for aldrin epoxidase. MpSWCB-4 on the other hand, had little effect on this enzyme, but appeared to stimulate aldrin epoxidase. The effect of MpSWCB-4 on insecticide susceptibility suggested that an activation reaction was occurring during the degradation of the organophosphate. Recommended rates of application of insecticides usually are determined from efficacy data for

the target insect without regard to the effects of the plant on which the insect was feeding. Results of experiments to determine the effect of MpSWCB-4 corn on insecticide susceptibility of FAW show that the influence of crops on the efficacy of insecticides varies. If resistant cultivars are to be incorporated into an IPM system for corn; effects of the cultivar on the pest, its natural enemies, and on its insecticide susceptibility must be known. This project should provide the basis and framework to stimulate future research on the subject of tri-trophic interactions and their role in pest management.

Plant resistance can play an important role in insect pest management. The development of crop plants resistant to insect attack should be an integral part of strategies for insect pest management. The role of plant resistance in a management program may be as a contributing feature or as a primary means of controlling a pest. Compatibility of natural enemies endemic to an area should be determined where possible. The performance of A. marmoratus was not affected adversely by MpSWCB-4 (resistant) cultivar. AM can be used in combination with MpSWcb-4. It would be useful to explore the possibility of "broadcasting" AM through irrigation water. The combined population reduction effects of AM and plant resistance of MpSWCB-4 would mitigate the need for chemical control. Studies on the impact of various pesticides used against FAW on corn, on natural enemies of

FAW are needed. Plant resistance in this study showed some incompatibility with insecticides, therefore it is sugested that plant resistance and natural enemies be used as strategies for IPM of FAW on corn.

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APPENDIX

TABLE A-1. Parameters for Determination of Performance Values

Parameter	Abbreviation	Formula
Relative Consumption Rate	R.C.R.	I/(MB x T)
Absolute Consumption Rate	A.C.R.	I/T
Relative Growth Rate	R.G.R.	B/(MB x T)
Absolute Growth Rate	A.G.R.	B/T
Approximate Digestibility (= Assimitation Efficiency)	A.D.	(I - F)/I
Efficiency of Conversion of Digested Food (= Net Growth Efficiency)	E.C.D.	B/(I -F)
Efficiency of Conversion of Ingested Food (= Gross Growth Efficiency)	E.C.I.	B/I

I = food ingested, mg. dry wt.
F = feces, mg. dry wt.
B = biomass gained, mg. dry wt.
MB = mean weight of the instar, mg. dry wt. = $\frac{Bf - Bi}{n(Bf/Bi)}$
T = duration of active growth stage, days

R.G.R. = R.C.R. x E.C.I.

E.C.I. = E. C. D. x A.D.

Table A-2. Larval duration and mortality of fall armyworm reared on diets containing silks of a resistant corn cultivar Zapalote Chico and a susceptible corn cultivar Stowell's Evergreen.

Diet	N	Mortality (%)	Larval duration (days)
Pinto bean (check)	30	3	15 c
Stowell's Evergreen	30	6	17 c
Zapalote Chico 5 g	30	3	21 b
Zapalote Chico 10 g	30	6	23 b
Zapalote Chico 20 g	30	6	33 a

In columns, values not followed by the same letter are significantly different ($p < 0.05$; Tukey's studentized range test)

TABLE A-3. Mean number of eggs laid by fall armyworm females reared on a pinto bean check diet (CK) and diets containing silks of Stowell's Evergreen corn (SEG) a susceptible cultivar, and Zapalote Chico corn (ZC) a resistant cultivar[a].

Diet	n	Mean number of eggs laid
Pinto bean (check)	10	1082.00 a (174.61)
Zapalote Chico 5 g	12	760.00 a (120.91)
Zapalote Chico 10 g	10	568.00 a (201.75)
Zapalote Chico 20 g	11	240.00 b (87.84)

Values expressed as mean (+/- Std. error); in columns, values not followed by the same letter are significantly different ($p < 0.05$; Scheffes).

Table A- 4 Mean percentage parasitization of fall armyworm larvae on whorl stage resistant corn (MpSWCB-4) and susceptible corn (Stowell's Evergreen) by Archytas marmoratus in Tifton, Georgia.

Cultivar/Plant Stage	1988 Mean Percent Parasitization	1988 N	1988 Percentage of Total Parasitization	1989 Mean Percent Parasitization	1989 N	1989 Percentage of Total Parasitization	Total Para 1988	Total Para 1989
Stowell's Evergreen/ 6-8 leaf stage	4.70 a (1.20)	28	15.30 b (3.50)	7.90 b (1.30)	24	95.60 a (4.40)	31.40 a (2.40)	8.70 a (1.7)
MpSWCB-4/ 6-8 leaf stage	8.10 a (1.60)	27	28.10 a (5.00)	13.60 a (1.90)	25	80.00 b (4.30)	27.0 a (2.10)	17.10 b (2.3)
Stowell's Evergreen/ 6-8 leaf stage	6.20 a (2.00)	26	21.80 a (6.30)	20.30 a (3.40)	23	100.00 a (0.00)	27.3 a (3.60)	20.30 (3.40)
MpSWCB-4/ 10-12 leaf stage	7.50 a (1.10)	26	40.00 a (6.00)	15.40 a (1.40)	26	66.00 b (8.70)	20.40 a (2.00)	27.30 (4.10)

Values expressed are mean (+/- std. error); in columns, values not followed by the same letter are significantly different ($p > 0.05$; Scheffe's) for each leaf stage, (6-8 or 10-12).

N= mean sample size for 10 replicates, rounded off to whole number.

TABLE A-5. Mean percentage parasitization of fall armyworm larvae on whorl stage resistant corn (MpSWCB-4) and susceptible corn (Stowell's Evergreen) by <u>Ophion</u> <u>flavidus</u> in Tifton, Georgia.

Cultivar/Plant Stage	1988 Mean Percent Parasitization	N	1988 Percent of Total Parasitization	1989 Mean Percent Parasitization	N	1989 Percent of Total Parasitization
Stowell's Evergreen/ 6-8 leaf stage	16.30 a (1.80)	28	54.20 a (6.70)	0.40 a (0.40)	24	2.00 b (2.00)
MpSwCB-4/ 6-8 leaf stage	10.70 b (1.40)	27	41.10 a (6.20)	3.10 a (1.00)	25	18.20 a (4.80)
Stowell's Evergreen/ 10-12 leaf stage	19.50 a (2.80)	26	73.20 a (5.60)	0.00 b (0.00)	23	0.00 b (0.00)
MpSWCB-4/ 10-12 leaf stage	12.90 a (1.90)	26	63.10 a (6.0)	11.90 a (3.70)	26	34.00 a (8.70)

Values expressed as mean (+/- std. error); in columns, values not followed by the same letter are significantly different ($p > 0.05$; Scheffe's) for each laf stage (6-8 or 10 12).
N= mean sample size for 10 replicates, rounded off to whole number.

Table A-6 Mean percentage parasitization of fall armyworm larvae on whorl stage resistant corn (MpSWCB-4) and susceptible corn (Stowell's Evergreen) by other parasites[a] and total percent parasitization[b] in Tifton, Georgia.

Cultivar/Plant Stage	1988 Total Percent Parasitization[b]	1988 N	1988 Percent of Total Parasitization By Other Parasites	1989 Total Percent Parasitization[b]	1989 N	1989 Percent of Total Parasitization By Other Parasites
Stowell's Evergreen/ 6-8 leaf stage	31.40 a (2.40)	28	30.50 a (6.50)	8.70 b (1.70)	24	2.00 a (2.00)
MpSWCB-4/ 6-8 leaf stage	27.00 a (2.10)	27	30.70 a (4.90)	17.10 a (2.30)	25	1.80 a (1.80)
Stowell's Evergreen/ 10-12 leaf stage	27.30 a (3.60)	26	5.00 a (2.50)	20.30 a (3.40)	23	0.00 a (0.00)
MpSWCB-4/ 10-12 leaf stage	20.40 a (2.00)	26	0.00 b (0.00)	27.30 a (4.10)	26	0.00 a (0.00)

Values expressed as mean (+/- std. error); in columns, values not followed by the same letter are significantly different ($p > 0.05$; Scheffe's).

[a] Other parasites included: Apanteles sp., Cotesia marginiventris (Cresson), Rogas laphygmae Viereck, Euplectrus comstockii Howard.

[b] Total includes Archytas marmoratus Townsend, Ophion flavidus Brulle, and other parasites.

N= mean sample size for 10 replicates, rounded off to whole number.

Table A-7. Mean pupal weights and eggs laid by fall armywom reared on whorl stage resistant (MpSWCB-4) and susceptible (Stowell's Evergreen) corn.

Diet	N	#eggs laid	N	FW (mg) pupae	DW (mg) pupae
Pinto bean (check)	12	1082 a (174.61)	27	-	81.89 (1.80)
SEG	11	881 a (181.85)	35	208.8 (4.9)	56.15 (3.9)
MpSWCB-4	19	410 b (100.68)	40	182.87 (11.13)	47.82 (1.9)

Values expressed as mean (+/- Std. error); in columns, values not followed by the same letter are significantly different ($p < 0.05$; Scheffe's). FW =fresh weight; DW = dry weight.

BIOGRAPHICAL SKETCH

Maude Francesca Christian-Meier was born in Lagos, Nigeria, West Africa, on the 15th of September 1956. She attended St. Theresa's Primary School in Accra, Ghana, from 1962 to 1966, and St. Mary's/Cathedral School in Kingston, Ontario, Canada from August 1966 to December 1968. She continued her education at Holy Child Secondary School in Cape Coast, Ghana, where she did O' and A' level General Certificate of Education examinations. She was the assistant senior prefect from 1973 to 1974.

In October of 1974 she began her undergraduate studies at the University of Ghana and was the student body treasurer from 1975 to 1976. She won the Angus Booth Memorial Prize in Zoology in 1977 and the Waddle Prize for Biological Sciences in 1978. Maude received her Bachelor of Science degree (second class upper division) from the University of Ghana in 1978 and stayed on to do National Service, as a teaching assistant in the Zoology Department. In August of 1981 she entered the University of Florida to

study entomology and received the Master of Science degree in 1985. Maude was the treasurer of the Entomology and Nematology Society of the University of Florida from 1984 to 1985. In January of 1986 she entered the program toward a doctoral degree in entomology at the University of Florida. She won an international fellowship from the American Association of University Women (AAUW) in 1988 and is a fellow of the AAUW.

Maude is married to Henry Meier and they have four children, Fernanda, Jack, Anthea, and Rachel.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Dr. C.S. Barfield, Chairman
Professor of Entomology and Nematology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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